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PLANT AND SOIL

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STUDIES IN MANURIAL VALUES OF SEAWEEDS

I. EFFECTS OF *PACHYMENIA HIMANTOPHORA* AND *DURVILLEA ANTARCTICA* MEALS ON PLANT GROWTH

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INTRODUCTION

Seaweeds have been used for manure from the earliest of times and in spite of the high cost of labour, they are still used today in many coastal districts of the world. These practices are, however, founded on very few precise and properly controlled experimental studies and frequently the manurial properties of a seaweed species have been evaluated purely by its chemical analysis. Much information is needed concerning possible effects of seaweed manures on the physical structure, microbiology, and chemistry of soils and consequently on plant growth. This paper reports investigations into the values of two species of seaweed commonly found in New Zealand: – *Pachymenia himantophora*, one of the largest Rhodophyceans, and *Durvillea antarctica*, a member of the Fucales.

METHODS

In all experiments, the seaweeds were applied to soils in the form of desiccated meals prepared by drying fresh material in the sun and subsequently at 105°C; this was then ground in an electric coffee grinder so that the resulting powder passed through a 2-mm mesh sieve.

All growth trials were carried out in pots under glasshouse conditions and in the majority of the experiments tomato seedlings (var. Potentate) were used as test plants. Seaweeds were found to affect germination and hence seeds were sown in silica sand: on emergence three seedlings were selected for uniformity and transplanted to each pot. The height of seedlings was found to be a fair indication of their growth and consequently this criterion was widely used; at the conclusion of each experiment the whole plants were harvested, dried at 105°C, and weighed.

The carbon content of plant material was determined by the Schollenberger-Allison wet-digestion method and the nitrogen by the micro-Kjeldahl technique. Phosphorus was estimated colorimetrically by the molybdenum-blue reaction, sulphur by precipitation as barium sulphate and chloride by the Titt & Holmes electrometric titration technique. The cations were analysed spectrophotometrically. The soil pH and chloride were estimated on a 1 : 5 (w/v) soil suspension using a Cambridge pH meter and the Titt & Holmes apparatus. Soil phosphate was extracted with 0.002 *N* sulphuric acid at pH 3 (buffered with ammonium sulphate) and determined colorimetrically. Exchangeable cations were leached out with 1 *N* ammonium acetate at pH 7 and estimated spectrophotometrically while the base-exchange capacity (B.E.C.) was determined by distilling the ammonia into boric acid after rinsing with ethanol.

RESULTS

Chemical composition of seaweed meals

The chemical analyses of the two seaweed meals show that *Durvillea* was considerably richer in cations and chloride than *Pachymenia* but poorer in nitrogen and sulphur (Table 1).

TABLE 1

Analyses of seaweeds used in experiments

Seaweed species	Date of collection	Ratio dry matter to wet weed		% dry matter		C/N ratio	% dry matter							M pp
		Stipe	Lamina	C	N		P	S	Cl	K	Na	Mg	Ca	
Pachymenia	19/3/55	—	—	—	1.84	—	0.11	—	—	1.11	4.41	0.80	0.50	<
	2/11/55	29.4	31.5	35.6	2.00	17.8	0.10	5.6	1.8	0.97	3.83	0.43	0.37	<
	10/2/57	32.7	31.5	36.4	1.55	23.5	0.10	5.6	1.7	0.95	3.84	0.59	0.37	<
Durvillea	19/3/55	—	—	—	1.06	—	0.12	—	—	1.55	5.26	1.21	1.56	
	2/11/55	18.6	19.6	32.2	0.98	32.9	0.12	0.7	5.7	2.08	5.28	1.17	1.50	<
	10/2/57	20.2	21.1	35.3	0.89	39.7	0.10	0.7	5.1	1.30	4.44	0.90	1.22	<

Effect of seaweed meals on the growth and mineral contents of tomato seedlings

Tomato seedling growth was found to be markedly affected by both the seaweed meals when added to a clay soil (pH 6.5) at different concentrations. *Durvillea* caused a depression in the growth rate which was more pronounced at higher concentrations (Fig. 1). High concentrations of *Pachymenia* also had an initial inhibitory effect but this was later reversed into a growth stimulation.

Growth trials carried out on five different soil types treated with

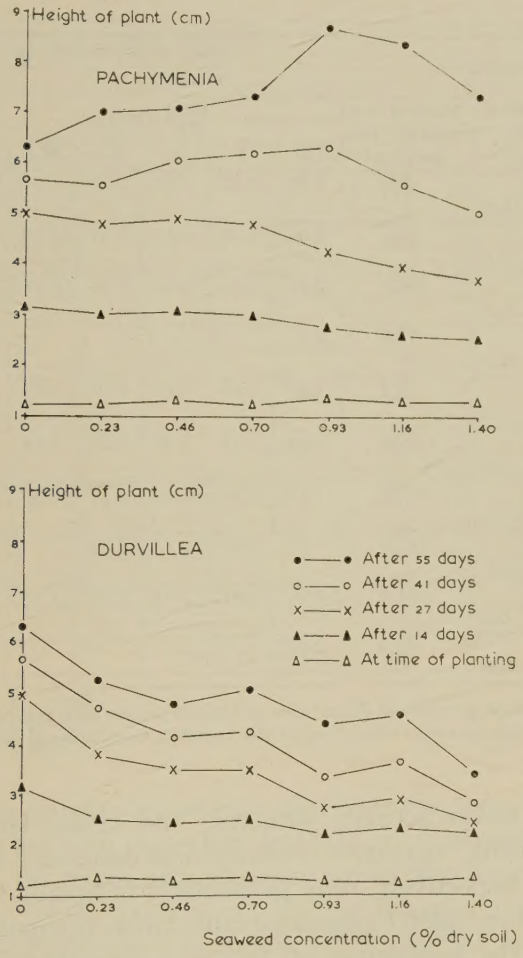

Fig. 1. Periodic measurements of tomato plants grown on soils with increasing seaweed concentrations on a clay soil (pH 6.5).

seaweed meals at the rate of 1.25 per cent (on a dry weight basis), showed that *Durvillea* had an inhibitory effect in every case (Table 2). *Pachymenia*, on the other hand, while stimulating growth on two of the soil types, had an inhibitory effect on the others; on two of the soils this growth depression was even more marked than that with *Durvillea*. Plants grown with *Pachymenia* developed darker foliage with a purplish tinge which usually became apparent within a week of planting out; they also exhibited lesions of dry tissue,

TABL

Expt. No.	Seedling age (days)	Soil type and pH	Yields of dry matter and mineral analyses of Control								
			Yield of dry matter (mg) per plant	% dry matter						ppm Mn	Yield matte plant
				N	P	K	Na	Mg	Ca		
6a	21	Clay 5.3	18.3	4.20	0.20	2.80	0.28	1.63	4.50	1588	14. (−20
6b	21	Sand 5.6	23.5	3.56	0.14	3.35	0.59	1.10	1.97	343	17. (−26
11	28	Loam 6.1	235.9	2.81	0.39	2.65	0.17	0.75	1.87	104	331. (+40
10	38	Clay 5.3	72.6	2.83	—	—	—	—	—	900	46. (−37
5a	44	Sand 5.6	79.7	1.95	0.18	2.43	0.22	0.85	2.27	209	13. (−83
5b	44	Clay 5.3	102.5	3.54	0.17	2.86	0.29	1.14	2.25	935	47. (−54
5c	44	Organic soil 5.2	313.0	1.74	0.20	2.46	0.11	0.57	1.78	248	138. (−56
2	55	Clay 6.5	151.5	1.08	0.21	1.77	0.22	—	2.53	100	373. (+147
3	55	Clay 6.5	81.0	2.09	0.41	2.53	0.35	1.13	3.72	138	176. (+118
G. 1	55	Clay 5.3	44.9	2.60	—	—	—	—	—	900	44. (

N.B. Figures in brackets denote percentage departures of treated plants with respect to controls.
Asterisks by figures indicate the degree to which departures of yields from those of control plants are stat significant.

some of the leaves actually withering and falling later (Fig. 2). These phenomena, suggestive of phosphorus deficiency and manganese toxicity respectively, were particularly noticeable on the soils with lower pH on which *Pachymenia* caused more pronounced growth depressions. The application of *Durvillea* was always associated with stunted growth (Fig. 2) and considerable yellowing of the foliage, very like that brought about by insufficient nitrogen supplies. In addition to the very striking differences observed in the leaves, seaweed-grown plants were found on harvesting to have marked differences in root development (Fig. 3).

Chemical analyses of tomato seedling leaves from the growth trials (Table 2) showed that there were some consistent differences in their mineral contents resulting from seaweed treatment. For plants grown on *Pachymenia*-treated soils, extremely high manganese contents were recorded; the highest levels were associated with

grown on untreated and seaweed-treated soils

Pachymenia							*Durvillea*						
% dry matter					ppm Mn	Yield of dry matter per plant (mg)	% dry matter						ppm Mn
P	K	Na	Mg	Ca			N	P	K	Na	Mg	Ca	
0.13 (−35)	2.47 (−12)	0.33 (+18)	1.62 (−1)	1.37 (−70)	2652 (+67)	17.5 N.S. (−4)	3.51 (−16)	0.17 (−15)	2.93 (+5)	0.53 (+89)	1.13 (−31)	4.50 (0)	1676 (+6)
0.13 (−7)	3.39 (+1)	0.69 (+17)	1.60 (+45)	2.07 (+5)	315 (−8)	12.2 (−48) **	2.37 (−33)	0.08 (−43)	2.53 (−24)	0.85 (+44)	1.00 (−9)	1.35 (−31)	88 (−74)
0.37 (−5)	2.95 (+11)	0.32 (+88)	0.79 (+5)	1.73 (−7)	187 (+80)	164.0 (−30) N.S.	3.08 (+10)	0.48 (+23)	2.87 (+8)	0.42 (+147)	0.94 (+25)	1.85 (−1)	90 (−13)
—	—	—	—	—	1792 (+99)	51.7 (−29) N.S.	2.26 (−20)	—	—	—	—	—	688 (−24)
—	—	—	—	—	—	15.3 (−81) **	1.48 (−24)	—	—	—	—	—	—
—	—	—	—	—	—	34.7 (−66) **	3.68 (+4)	0.18 (+6)	2.37 (−17)	0.47 (+62)	1.57 (+38)	2.90 (+29)	1308 (+40)
0.23 (−15)	3.11 (+26)	0.23 (+109)	1.03 (+81)	2.33 (+31)	1488 (+500)	129.3 (−59) **	2.32 (+33)	0.22 (+10)	2.40 (−2)	0.32 (+191)	0.66 (+16)	1.98 (+11)	154 (−38)
0.23 (+10)	2.13 (+20)	0.32 (+45)	0.80 (−)	2.04 (−19)	214 (+114)	75.6 (−50) *	2.10 (+94)	0.30 (+43)	1.50 (−15)	0.70 (+218)	—	2.87 (+13)	—
0.28 (−32)	3.41 (+35)	0.38 (+9)	1.68 (+49)	2.84 (−24)	343 (+149)	35.9 (−56) N.S.	3.74 (+79)	0.43 (+5)	2.73 (+8)	1.20 (+243)	—	3.91 (+5)	133 (−4)
—	—	—	—	—	1706 (+90)	33.4 (−26) N.S.	1.87 (−28)	—	—	—	—	—	487 (−46)

nsignificant at the 5% level.
gnificant at the 5% level.
gnificant at the 1% level.

considerable growth depressions. The leaf symptoms (occurrence of lesions coupled with premature leaf fall) are in accordance with the theory that the increased manganese uptake was toxic to growth. In the majority of the experiments the leaf nitrogen was considerably increased by *Pachymenia* treatment indicating that the seaweed may be capable of making this element quickly available to the plant. Young seedlings grown on *Pachymenia*-treated soils appear to have had lower phosphorus levels which could account for the observed changes in the pigmentation of the leaves. As may be expected sodium contents were in all cases higher. The *Pachymenia* treatment produced only minor changes in the potassium, magnesium, and calcium contents.

Increase in the sodium content of plants grown on *Durvillea*-treated soils is the salient feature of the leaf analysis data whereas the other cations show only relatively small differences from the

Fig. 2. The leaf morphology of tomato plants (21 days old) grown on untreated sandy soil (above) and that treated with *Pachymenia* (middle) and *Durvillea* (below) meals at the rate of 1.25%.

control plants. Phosphorus appeared to be lower in young plants and higher in older ones as did the nitrogen, although the results lack consistency. The relatively low nitrogen contents in leaves of young plants may explain why these showed yellowing in the initial stages of growth.

Effect of seaweed meals on soil physical conditions

Whereas *Durvillea* meal did not noticeably appear to affect soil physical conditions, *Pachymenia* was observed to have a detrimental effect on the soils with pH less than 6. These soils assumed a gelatinous consistency, became impermeable to water and remained waterlogged for long periods.

Effect of the time of application of seaweed meals

An experiment was carried out in order to determine whether a delay in

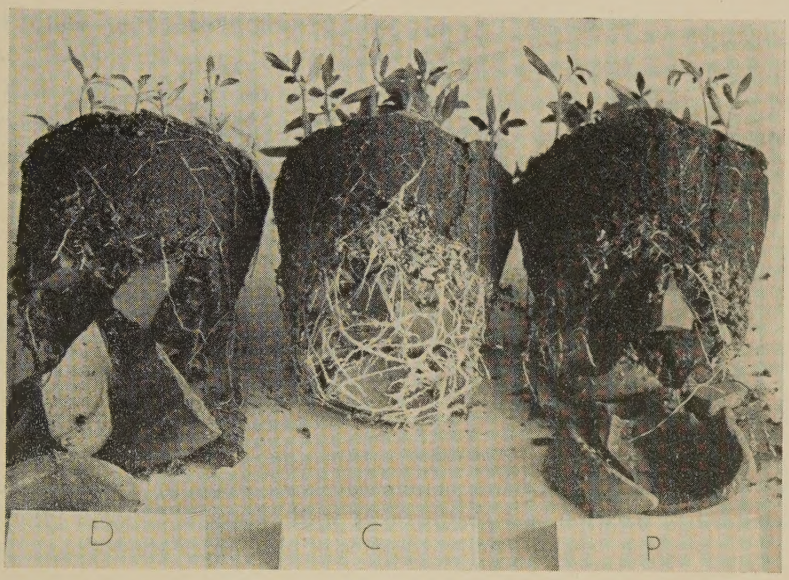

Fig. 3. The root development of tomato plants (21 days old) grown on *Durvillea* treated (D), untreated (C), and *Pachymenia* (P) treated sandy soil. (Seaweed treatment at the rate of 1.25%. Twenty plants grown in each pot).

planting out of tomato seedlings, following the application of seaweed meals to soil, would reduce the initial inhibition of plant growth. Twenty-two days prior to the planting out of the seedlings, the clay soil used (pH 6.5) was divided into five portions. One portion was treated by thorough mixing with *Pachymenia* and one with *Durvillea* meal at the rate of 1.25 per cent, then all five portions were potted into 4″ pots, arranged in a latin square in the glasshouse, and watered regularly as if plants were growing in them. Just prior to planting out all the soils were removed from their pots and to two of the untreated portions seaweed meals were added, again at the rate of 1.25 per cent. The soils were then returned to their pots and tomato seedlings planted. Soils treated with seaweeds 22 days prior to planting out are referred to as leached, and those treated just prior to planting out as unleached. Soil samples were taken for analysis at the time of planting and leaf samples after harvesting (55 days after planting).

The results show that the length of time between applying the *Pachymenia* meal to the soil is immaterial while that of *Durvillea* is of considerable importance (Fig. 4). It is evident that the initial growth inhibition caused by seaweed meals, although lessened, is not overcome by delaying the planting out of seedlings after seaweed application. As before, differences in foliar pigmentation became

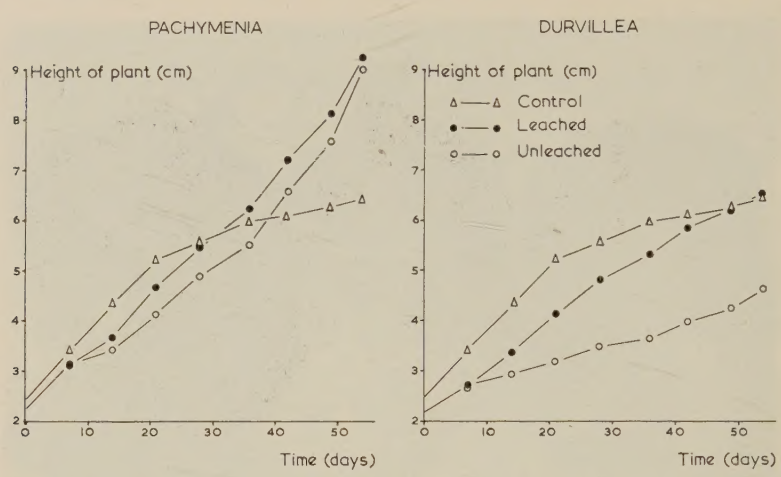

Fig. 4. Periodic measurements of tomato plants grown on untreated clay soil (pH 6.5) (control) and that treated with seaweeds 22 days prior to planting (leached) and at the time of planting (unleached).

evident at an early stage, but the yellowing of plants grown on *Durvillea*-treated soil disappeared very much more rapidly in plants grown on the leached soil. The soil sodium-chloride concentration was considerably increased by the addition of seaweed meals, especially in the case of *Durvillea* (Table 3), but considerable leaching from soils treated with seaweeds prior to planting out was evident. The sodium content of *Durvillea*-grown plants on unleached soil

TABLE 3

Soil analyses carried out at the time of planting out seedlings									
Treatment	Milliequivalents per 100 g air-dry soil							P as avail. PO_4^{---} ppm	pH
	B.E.C. *	T.E.B. **	Na^+	K^+	Mg^{++}	Ca^{++}	Cl^-		
Control	23.1	19.0	1.27	0.45	7.6	9.6	0.42	23	6.6
Pachymenia unleached	23.3	20.6	2.78	0.60	7.5	9.7	1.02	22	6.4
Pachymenia leached	23.6	20.3	2.45	0.60	7.5	9.7	0.77	23	6.3
Durvillea unleached	24.2	23.0	3.67	0.81	7.9	10.6	2.47	24	6.4
Durvillea leached	23.4	21.1	3.07	0.65	7.4	9.9	1.67	23	6.8

* B.E.C. = Base-exchange capacity.
** T.E.B. = Total exchangeable bases.

was much higher than that of the others (Table 4). It is surprising that plants grown on *Durvillea*-treated soils possessed higher levels of nitrogen than those on untreated, however, at the time of harvesting all symptoms suggesting nitrogen deficiency had disappeared.

TABLE 4

Leaf analyses carried out on harvested tomato plants							
Treatment	Per cent of dry leaf matter						ppm
	N	P	K	Na	Mg	Ca	Mn
Control	2.09	0.41	2.53	0.35	1.13	3.72	138
Pachymenia unleached	3.50	0.28	3.41	0.38	1.68	2.84	343
Pachymenia leached .	3.49	0.34	3.81	0.41	1.31	2.64	489
Durvillea unleached .	3.74	0.43	2.73	1.20	0.67	3.91	133
Durvillea leached . .	3.13	0.41	2.81	0.54	1.00	3.53	106

These results suggest that the growth of tomato plants on *Durvillea*-treated soil may be adversely affected, either by its relatively high salt content or else by an initial, temporary nitrogen deficiency.

The effect of seaweed salt on plant growth

Experiment (a)

In this experiment three crops of different salt tolerance, as classified by Richards [8], were grown: radish (salt intolerant) tomato (medium tolerance), and beetroot (salt tolerant). Since *Durvillea* was found to be considerably richer in salts than *Pachymenia* and did not appear to bring about manganese toxicity, as does the latter, it was the only seaweed used in this experiment. Each of the three crops was grown with and without *Durvillea* meal applied at the rate of 1.25 per cent on a clay soil (pH 5.3).

Differences between plants grown on treated and untreated soils were observed within a week of planting out; those of the beetroots were the most extreme, the treated plants being very stunted. In all three crops there were striking changes in foliar pigmentation; tomato and radish plants on treated soil showed leaf yellowing while the beetroots appeared paler and the red pigment was not as well developed as in the control plants. Four weeks after planting out the two sets of tomato seedlings appeared comparable in size, but the foliage of the *Durvillea*-treated plants remained paler. Radishes on the untreated soil had healthy foliage and swollen roots, whilst those on the treated were much poorer and their roots

had not started to enlarge. The growth differences in the beetroots were the most striking.

Thus *Durvillea* meal had a detrimental effect on all the crops, and the effect was at least partly due to factors other than the salt concentration, since the salt-tolerant beetroot was the most markedly affected.

Experiment (b)

In this experiment tomato plants were grown in clean river sand watered with *Durvillea* extracts and mineral-salt solutions, in order to find out if the salt contained in the seaweed is responsible for growth inhibition. Different concentrations of *Durvillea* extracts were prepared by shaking the seaweed meal in water overnight on a mechanical soil shaker. Other batches of plants were grown and watered with sodium chloride and potassium chloride solutions, using chloride concentrations equivalent to those of the *Durvillea* extracts. Plants were watered with 50 ml of their respective solutions every 10 days, and in between these periods they were watered with a full nutrient solution (Long Ashton formula – Hewitt [3]) so as to eliminate any possible complications due to mineral deficiencies. The seedlings were grown for 25 days and during this time they were watered twice with the full nutrient solution and three times with the extracts or their chloride equivalents.

The plants grown in sand watered with *Durvillea* extracts failed to show the foliage symptoms which were characteristic of seedlings grown in soil with *Durvillea* meal, therefore if the leaf yellowing was indeed caused by nitrogen starvation as suggested, then it seems that the mechanism responsible for the removal of this element must have been absent in sand. Dry weights of the harvested plants are plotted in Fig. 5. Statistical analysis showed that only *Durvillea* extracts, and only at concentrations above 0.5%, induced significant depressions of growth in seedlings.

DISCUSSION

The effects of seaweed meals on soil conditions, and consequently on plant growth, could be due to one or a combination of any of the following factors:

(1) Changes in the ionic content of the soil.
(2) Changes in the physical structure of the soil.
(3) Presence of organic compounds affecting growth.
(4) Effects on the soil micro-organism population.

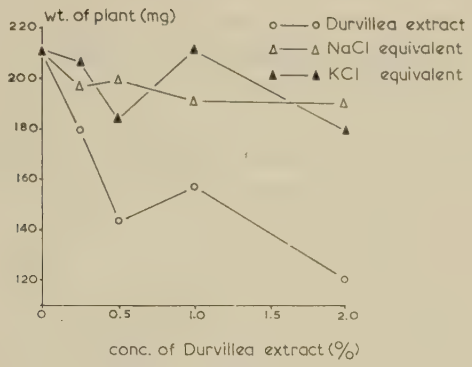

Fig. 5. Yields of dry matter harvested from tomato plants grown in sand culture and watered with *Durvillea* extracts and their chloride equivalents after 25 days' growth.

The most marked change in the ionic content of soils following seaweed treatment was in the sodium chloride content, yet this alone has been shown not to be responsible for growth inhibition. Plice [7] has similarly found that dressings of up to 4 tons of sodium chloride per acre under field conditions (approximately 0.45 per cent) were not detrimental to the growth of tomatoes. *Durvillea* applied at the rate of 1.25 per cent is equivalent to approximately 0.25 per cent of sodium chloride. It is possible, however, that seaweed salts may increase the osmotic pressure of the soil solution to levels unfavourable to plant growth. This requires investigation.

One of the most striking results of treating soil with *Pachymenia* was the increase of manganese taken up by the test plants; this was probably great enough to have been toxic. The meal itself had less than 4 ppm of manganese so it could not have provided the excess manganese taken up, but must have caused its release in an available form from that already present in the soil. It is well established that acid soil conditions cause available manganese to reach high concentrations, as do reducing conditions through excess organic matter, waterlogging, or compaction (Page and Bodman [5]). Addition of oxidisable sulphur compounds (Garey and Barber [2]) and large amounts of chloride (Sherman *et al.*[9]) also cause trivalent manganese to be reduced to the divalent, available form. The addition of *Pachymenia* meal to soil can contribute to all of the above factors and their relative importance is still under investigation.

Little work has been done on growth factors and inhibitors present in algae although growth-promoting substances, auxins, antibiotics and growth inhibitors have all been found in certain species. Although at present there is no conclusive evidence that either *Pachymenia* or *Durvillea* possess organic compounds that affect growth, it is definitely a possibility that must be considered.

In treating soil with seaweed meal much organic matter is added which must have a considerable effect on the soil micropopulation. There is ample evidence in the literature, recently reviewed by Winsor [10], that the rotting of material with high C/N ratio lowers the inorganic nitrogen resources of the soil due to transformations into microbial organic forms. The effect of the two seaweed meals on soil nitrogen metabolism has been investigated and reported separately (Francki [1]).

An effect of organic matter on soil rather similar to that of micro-organism-induced nitrogen deficiency has been reported by Kaila [4] for phosphate. She concluded that decomposing organic matter must contain about 0.2 per cent of phosphorus if the needs of micro-organisms for this element are to be satisfied; both *Pachymenia* and *Durvillea* fall short of this, having only about 0.1 per cent. The appearance of *Pachymenia*-grown plants did suggest a phosphorus deficiency while in the case of *Durvillea* the yellowing of the plants may well have masked this symptom. Analyses of very young leaves showed that seaweed-grown plants had actually lowered phosphorus levels. Investigations into this problem are still required.

Stimulated activity of soil micro-organisms is also known to affect plant growth in other ways. Parbery and Swaby [6] found that lucerne, when applied in quantity to soil, subsequently had a toxic effect on crops. They came to the conclusion that the toxic substance was not present in the plant material, but was formed during its decomposition. Such a condition is unlikely in the case of *Pachymenia* and *Durvillea* as plants grown on soils treated with them exhibited an initial depressed growth rate which was later at least partially overcome. Page and Bodman [5] believe that the commonly observed depression in plant growth immediately after adding large amounts of organic manure to a soil may be due to competition for oxygen between the higher plants and micro-organisms rather than to any other single factor. This phenomenon may well be operating when seaweeds are used as fertiliser.

Effects of *Pachymenia* and *Durvillea* on plant growth involve quite diverse phenomena, showing that generalised statements about manurial values of seaweeds should be made with the utmost caution and should not be based purely on the chemical analysis of a species. Only comprehensive experimentation can give a true indication of a seaweed's manurial value.

SUMMARY

Investigations have been undertaken into the manurial values of two New Zealand seaweed species, *Pachymenia himantophora* (Rhodophyceae) and *Durvillea antarctica* (Phaeophyceae). Chemical analyses have shown that *Durvillea* is richer than *Pachymenia* in cations and chloride but poorer in nitrogen and sulphur. When applied to soil in the form of dry meal *Pachymenia* was found to stimulate the growth of tomato seedlings on some soils and depress it on others; *Durvillea*, on the other hand, depressed growth on all the soil types used. Experiments indicated that the salts contained in the seaweeds were not harmful to plant growth.

Pachymenia may be inhibitory to plant growth on some soils through causing a greatly increased manganese uptake and there was an indication that in treated soils the level of available phosphate was lowered, at least initially. *Durvillea* is thought to induce nitrogen deficiency in soils by virtue of its high C/N ratio; this is, however, unlikely to be the sole factor responsible.

Effects of seaweeds on soil conditions are complex and can involve many factors: the manurial values of a species cannot be judged solely on its mineral analysis.

ACKNOWLEDGEMENTS

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Plant and Soil XII, no. 4 June 1960

STUDIES IN MANURIAL VALUES OF SEAWEEDS

II. EFFECTS OF *PACHYMENIA HIMANTOPHORA* AND *DURVILLEA ANTARCTICA* ON THE IMMOBILISATION OF NITROGEN IN SOIL

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INTRODUCTION

The results of growth-trial experiments carried out under glasshouse conditions reported in the previous paper (Francki [2]) indicated that plants grown on soils freshly treated with dry meal from *Durvillea antarctica*, a seaweed species with high C/N ratio, may have been suffering from inadequate nitrogen supplies. It was suggested that this may have been due to biological immobilization of the inorganic nitrogen present in the soil. *Pachymenia himantophora*, the other seaweed species used, had a higher nitrogen content and did not induce any signs of nitrogen starvation in plants. This paper reports results of investigations into the levels of inorganic nitrogen and microbiological activity in soils following seaweed traetment.

METHODS

Glasshouse trials

The techniques used in growth trials were identical with those already reported (Francki [2]).

The soil-percolation technique

With the exception of the air-supply equipment, the apparatus used was essentially like that of Lees [5]. Sterile, moist air was supplied intermittently by an electric pump, switched on and off by a simmerstat, through two winchester bottles of scrubbing fluid (5% w/v copper sulphate in 2.5% v/v

sulphuric acid) into twelve percolators housed in a constant-temperature cabinet kept at 25 ± 1°C.

Fresh soil samples brought up to field capacity, and equivalent to 50 g dry weight, plus 200 ml of fluid were used in each percolator. Before samples of the percolation fluid were removed for analysis, evaporation losses were compensated for by adding distilled water; the quantities required were always small. No compensations were made for the volumes of liquid withdrawn as samples but after each sample was taken the air supply to each percolator was re-adjusted to ensure steady percolation. This procedure had the disadvantage of decreasing the ratio of perfusate volume to soil volume; on the other hand, progressive dilution of the perfusate was avoided. For purely comparative purposes, as in this work, this procedure was quite adequate.

Using this technique the nitrogen changes in three soils, each untreated and treated with seaweed meals at the rate of 1.25 per cent, was followed over periods of 70 days. At the commencement of each experiment the percolation fluid consisted of a solution of ammonium nitrate and di-ammonium hydrogen phosphate which gave concentrations of 110 ppm ammonium nitrogen, 100 ppm nitrate nitrogen and 11 ppm phosphate phosphorus * respectively. In the soil, nitrate and nitrite ions are considered to be present exclusively in solution and thus, by analysing the perfusate, their formation or destruction in the soil can be estimated accurately. Ammonium ions, however, are partly in solution and partly adsorbed on to the soil colloidal particles so that the analysis of the perfusate only accounts for a portion of them. Lees and Quastel [8] have shown experimentally that the ammonium "adsorption ratio" ** remains reasonably constant throughout a normal nitrification experiment and hence for comparative purposes it is sufficient to analyse the perfusate only for ammonium nitrogen. The total inorganic nitrogen was calculated by adding the values obtained for ammonium nitrogen and nitrate nitrogen in the perfusate. The nitrite content was always found to be very low in relation to the ammonium and nitrate and was therefore ignored.

Analytical techniques

The ammonium and nitrite concentrations were estimated colorimetrically by the Nessler and α-naphthylamine–sulphanilic acid methods respectively [1] on small samples of the perfusate (0.5 to 3 ml, according to the concentrations present) diluted to 25 or 50 ml. The colour intensities were read on a Hilger Spekker absorptiometer.

The nitrate was estimated by a modification of the indigo method described by Sutton [8]. A sample of perfusate (0.5 to 3 ml) was made up to

* Phosphate was added in the hope of simultaneously following the phosphorus metabolism of the soils; experimental difficulties made this impossible.

** The ammonium "adsorption ratio" is defined by Lees as:

$$\frac{\text{Ammonium nitrogen bound in soil exchange complex}}{\text{Total ammonium nitrogen in the system}}$$

10 ml with distilled water in a 50-ml Erlenmeyer flask, and 10 ml of concentrated sulphuric acid (nitrate free) was added from a long graduated separating funnel down the side of the flask. The two liquids were mixed by agitation and the hot solution was titrated with indigo carmine reagent * to a permanent blue colour using a 1-ml burette. Nitrites, when present in high concentrations have been reported to interfere with the analysis but in this study they were always found to be low.

Measurement of oxygen uptake by soils

The microbiological activity of soils was investigated by measuring their oxygen uptake using an apparatus similar to Jackman's[3] modification of Swaby and Passey's[9] model (Fig. 1). With this apparatus, when connected to a D.C. supply (12 volt), the quantity of oxygen taken

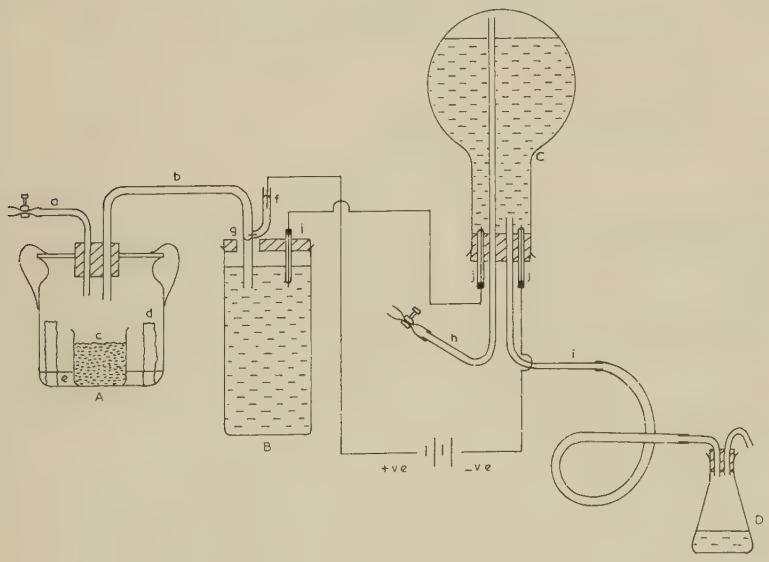

Fig. 1. Macrorespirometer used for measuring the oxygen uptake by soils.

A – respiration chamber
B – acid jar
C – acid reservoir
D – collecting flask

a – pressure regulating tube
b – electrode side arm
c – beaker with soil
d – filter paper
e – KOH solution
f – HgJ tube
g – Pt electrode
h – inlet tube
i – outlet tube
j – Pt electrode

* Indigo carmine reagent was prepared by adding one drop of concentrated sulphuric acid to 10 ml of distilled water to 0.4 gm of indigo carmine. After leaving overnight, the solution was made up to 100 ml. The reagent was always checked against standard potassium nitrate before use.

up by the respiring system (c) can be calculated from the weight of 1 N sulphuric acid displaced into the collecting flask (D). As the respiring system takes up oxygen, carbon dioxide given off is absorbed by potassium hydroxide solution (15% w/v). The change of pressure thus created causes a rise in the level of acid in the electrode side arm (b) which comes into contact with the platinum electrode (g). This closes the electrical circuit and current flows bringing about the electrolysis of sulphuric acid (in the acid jar B and reservoir C) liberating oxygen into the respiration chamber (A) and both hydrogen and oxygen into the acid reservoir (C). The volume of oxygen at N.T.P. taken up can be calculated from the formula:

$$A = \frac{273 P_1 x}{760 T_1 W \rho^3}$$

where:

A = Vol. of O_2 at N.T.P. in cc taken up per g of dry soil.
P_1 = Observed atmospheric pressure (mm Hg).
x = Wt. of acid expelled from reservoir (g).
T_1 = Observed temp.
W = Dry wt. of soil sample (g).
ρ = Sp. gr. of H_2SO_4 in reservoir.

In experiments, fresh soil samples equivalent to 50 g dry weight, or less in the case of very active soils, were used in each respirometer unit after they had been placed into 100-ml beakers and their moisture contents brought up to the required levels by the addition of water. After assembly the complete respirometer units were left for 2 to 3 hours for the temperature to equilibrate before the levels of acid in the electrode side arms were adjusted by suction to touch the platinum electrodes. Collecting flasks were weighed at intervals ranging from one to several days, depending on the activity of the soil examined. At the end of each experiment the beakers of soil were dried at 105°C, cooled, and weighed.

In every experiment each treatment was replicated four times and this normally gave a mean value with a standard error well below 10 per cent. It was found that temperatuie control to within 1°C was essential in order to avoid sucking back of acid into the respiration chamber and more particularly of air into the reservoir.

Soil micro-organism counts

The numbers of bacteria and fungi in soils were estimated by the plating technique (Waksman [10]). Bacteria were counted on Thornton's agar and fungi on Waksman's medium to which 1 part in 15,000 of Rose Bengal was added as a bactericide (Smith and Dawson [7]).

RESULTS

Glasshouse trials

Tomato seedlings were grown for 28 days on a good loam soil (pH 6.1 and C/N ratio of 10.3) immediately after treatment with

1.25% *Pachymenia* and *Durvillea* meals. Half the pots of each treatment were watered at the commencement of the experiment and again 14 days later with 50 ml of 0.02 *M* ammonium nitrate.

Within ten days of planting out seedlings showed slight differences in appearance. Plants on the untreated soils and those treated with *Pachymenia* seemed to have responded slightly to the added nitrogen. Seedlings on *Durvillea*-treated soil which were poor in comparison with those untreated showed considerable stunting and slight yellowing of leaves especially of the cotyledons, but exhibited a marked response to the addition of nitrogen. In later stages of the experiment, the responses to ammonium nitrate were very pronounced on soils of all the treatments but the most noticeable was on that treated with *Durvillea* (Table 1).

TABLE 1

Effects of seaweed meals and added ammonium nitrate on the yields of dry matter of tomato plants after harvesting

Treatment		Yield dry matter per plant (mg)	Increase over control † %	Increase over unfed ‡ %
Seaweed added	Feeding			
Untreated	Control	235.9	—	—
	NH_4NO_3	386.1	+64 **	+64 **
Pachymenia . . .	—	331.4	+40 *	—
	NH_4NO_3	471.5	+100 **	+42 **
Durvillea	—	164.0	−30 N.S.	—
	NH_4NO_3	401.9	+70 **	+145 **

† Plants grown on untreated and unfed soil are taken as control.

‡ Plants grown on seaweed-treated or untreated soils unsupplemented by other nutrients are taken as unfed.

Asterisks indicate the degree to which departures of yields from those of control or unfed plants are statistically significant:

N.S. Insignificant at the 5% level.

* Significant at 5% level.

** Significant at 1% level.

If a micro-organism-induced nitrogen deficiency is the only factor responsible for depression of plant growth in *Durvillea*-treated soils, then it should not become evident in a crop fixing nitrogen symbiotically. Pea seedlings were grown on two different soil types on which it was previously found that *Durvillea* reduced the growth rate of tomato seedlings inducing the usual leaf symptoms suggesting nitrogen deficiency. With the peas *Durvillea* had a slight

inhibitory effect which was statistically significant on one of the soils, there were, however, no adverse leaf symptoms.

Soil percolation experiments

In the sandy soil (see Table 2 for analysis) all inorganic nitrogen transformations were slow (Fig. 2). In the untreated sample there

TABLE 2

Analyses of soil types used in percolation experiments					
Soil type	% C	% N	C/N ratio	pH	O_2 uptake * cc/g over 72 h at 26°C
Sand	2.2	0.14	16.0	5.6	0.06
Organic soil . .	5.8	0.31	18.8	5.2	0.62
Loam	3.6	0.35	10.3	6.1	0.98

* Oxygen uptake of soils was determined on fresh samples (25 to 50 gms) to which sufficient water was added to bring them up to 70% of their field capacity.

was very little change in the total inorganic nitrogen throughout the experiment and the rate of nitrification, as judged by the removal of ammonia and production of nitrate, was slow. In both the seaweed-treated samples the total inorganic nitrogen content of the perfusate was significantly depressed, especially in the initial stages of the experiment. In the *Pachymenia*-treated sample the ammonium level was, throughout the experiment, somewhat higher than in the untreated and the nitrate reached rather low levels, expecially in the initial stages of the experiment. This may have been a result, either of retarded nitrification, or of stimulated ammonification coupled with increased biological uptake of nitrate, or possibly a combination of both these phenomena. In the *Durvillea*-treated sample the rate of disappearance of ammonia, in particular at the initial stages of the experiment, was more rapid than either in that of control or *Pachymenia*; changes in the nitrate, however, were intermediate between the two.

On the organic soil, which is biologically more active (Table 2), the nitrification was more rapid (Fig. 3). *Pachymenia* treatment caused the ammonium concentration of the percolating fluid to be higher than that of the control and the nitrate content dropped rapidly almost to zero, then recovered slowly, although it never reached the concentration present in the untreated soil. Even

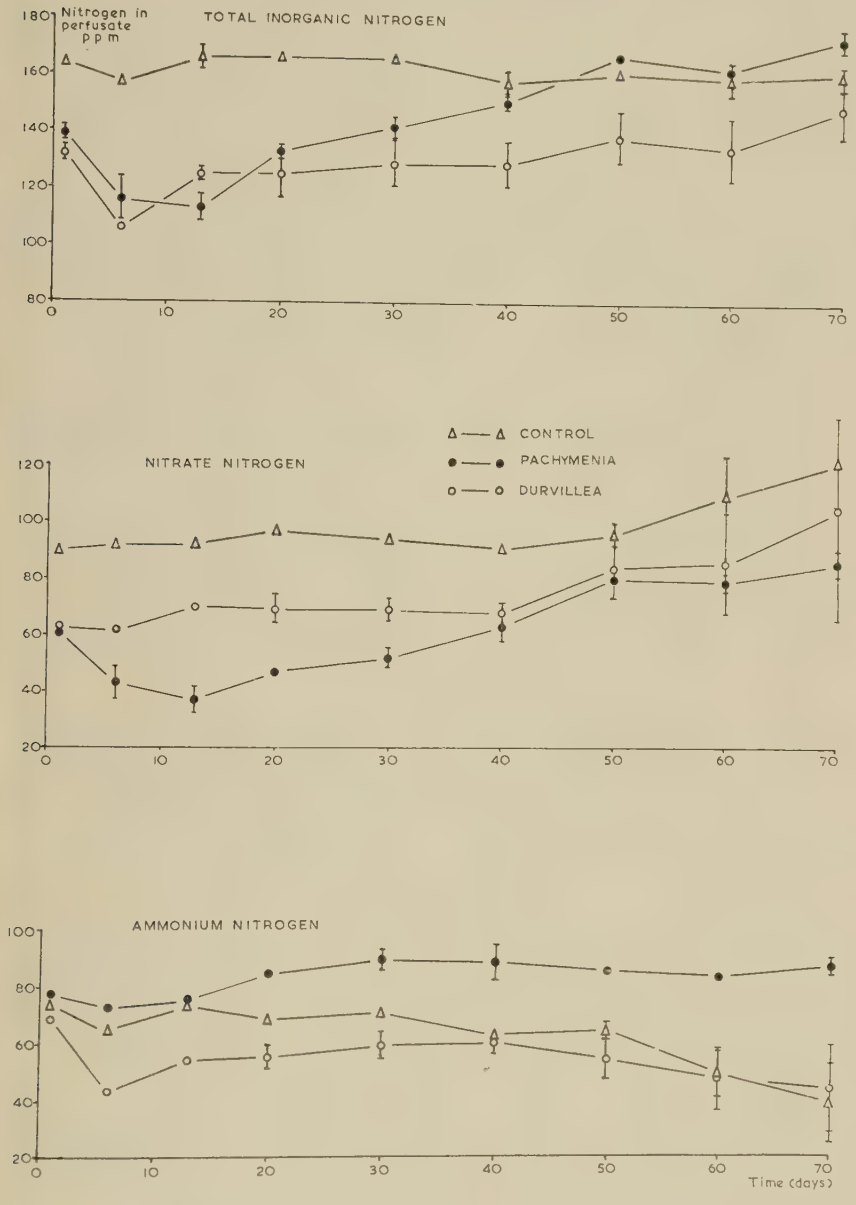

Fig. 2. The effect of seaweed meals on the inorganic nitrogen (ppm) of sandy soil. (Vertical lines represent twice the magnitude of the standard errors of the means).

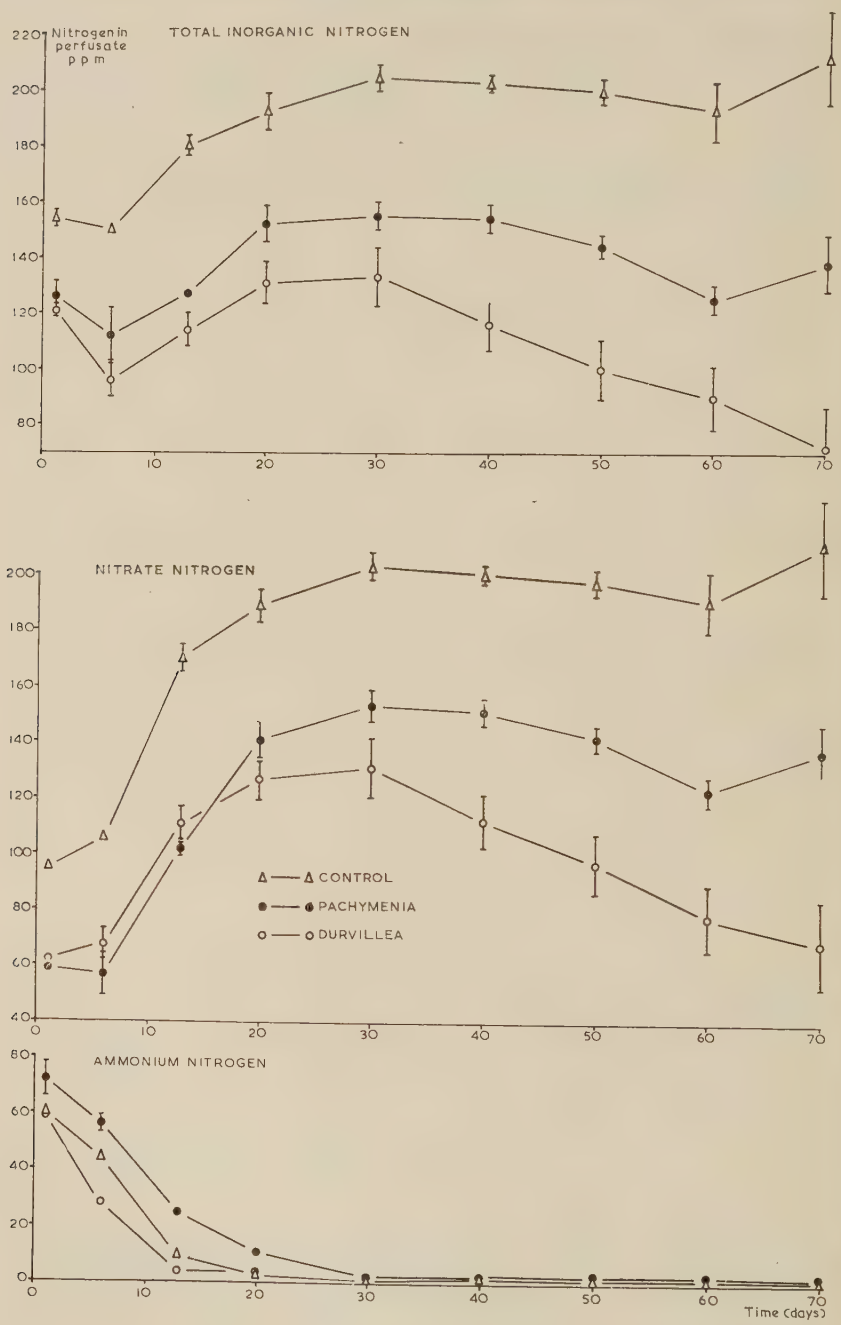

Fig. 3. The effect of seaweed meals on the inorganic nitrogen (ppm) of organic soil. (Vertical lines represent twice the magnitude of the standard errors of the means).

after 70 days both the nitrate and total inorganic nitrogen in the percolation fluid were less than 60 per cent of that in the untreated samples. *Durvillea* appeared to have stimulated nitrification (as shown by the disappearance of ammonia) and caused the almost complete removal of nitrate from the percolating fluid after 25 days which remained at a negligible level for the rest of the experiment.

On the loam, biologically the most active soil studied (Table 2), both nitrification (as shown by the ammonium and nitrate curves in Fig. 4) and nitrogen mineralization (as shown by the total inorganic nitrogen formation), were very rapid. Neither of the two seaweeds caused such a significant initial drop in nitrate as found on the other two soil types. The most striking effect of the seaweeds on this soil was on the loss of nitrate, and consequently total inorganic nitrogen, in the later stages of the experiment, in particular in the case of *Durvillea*. This suggests that possibly the seaweed treatments had stimulated denitrification.

It was shown that the soil nitrogen transformations were the result of microbiological activity as they could be inhibited by adding mercuric chloride to the perfusates at a concentration of 0.1 per cent.

The activity of micro-organisms in seaweed-treated soils

Pachymenia and *Durvillea* meals, when added to soils at the rate of 1.25 per cent caused considerable increases in their respiratory activities as shown by the oxygen uptake data in Table 3.

TABLE 3

The effect of seaweed meals on the oxygen uptake of soils over four days at 25°C and at a moisture of 70% field capacity

Soil type	Control	*Pachymenia*		*Durvillea*	
	O_2 uptake cc/g over 4 days	O_2 uptake cc/g over 4 days	Increase over contr. %	O_2 uptake cc/g over 4 days	Increase over contr. %
Sand	0.08	0.68	+750	1.22	+1,425
Organic soil . . .	0.76	1.48	+95	1.68	+121
Loam	1.48	2.38	+61	2.48	+68

On all three soil types studied *Durvillea* had a more pronounced effect in increasing the oxygen uptake than did *Pachymenia*.

Bacterial and fungal counts on seaweed-treated and untreated

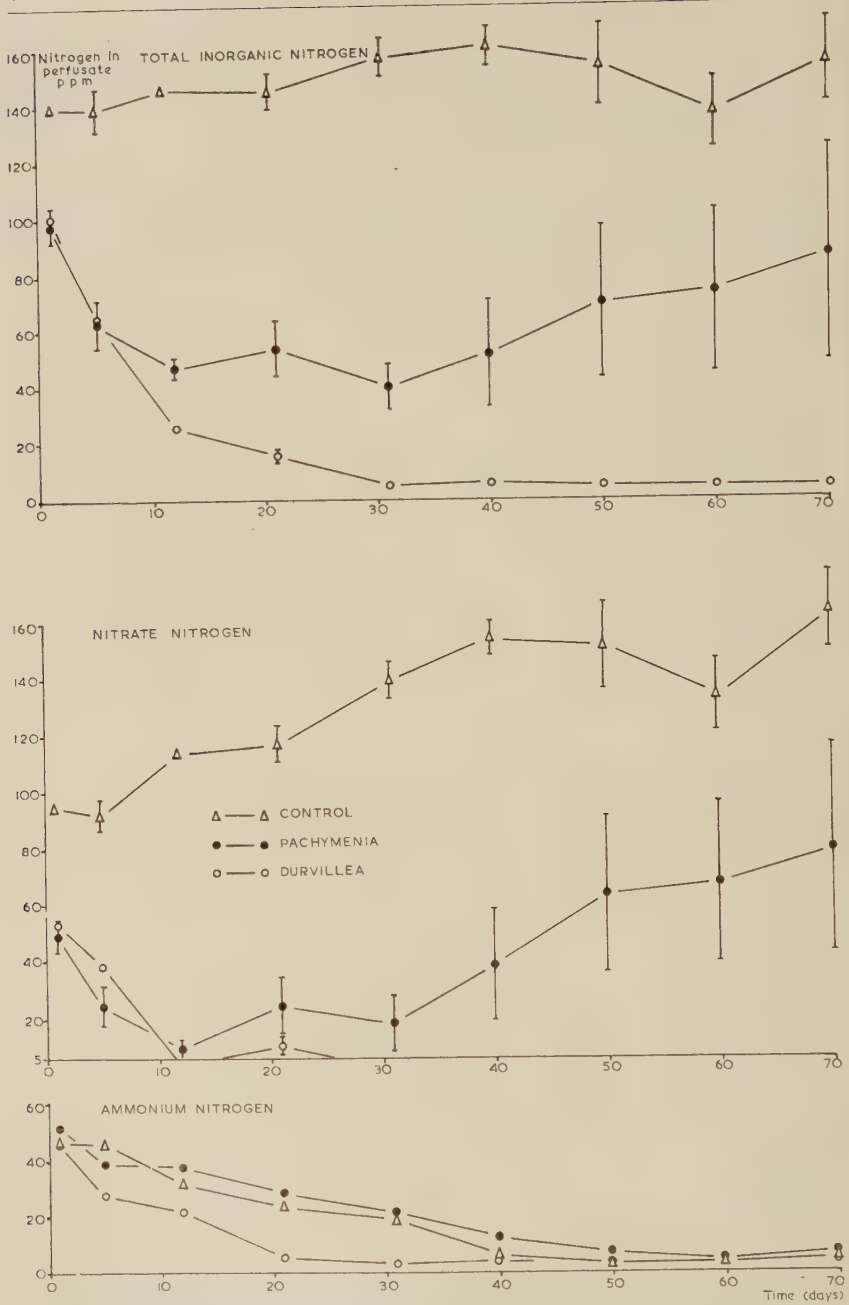

Fig. 4. The effect of seaweed meals on the inorganic nitrogen (ppm) of loam. (Vertical lines represent twice the magnitude of the standard errors of the means).

soils showed that 10 days after treatment the micro-organism population had built up considerably in numbers (Table 4). With

TABLE 4

The effect of seaweed meals on the micro-population of two soils after ten days' incubation at 25°C and moisture of 70% field capacity

Soil type	Control		*Pachymenia*		*Durvillea*	
	Bacteria × 10^6/g	Fungi × 10^6/g	Bacteria * × 10^6/g	Fungi * × 10^6/g	Bacteria * × 10^6/g	Fungi* × 10^6/g
Sand	3.2	0.5	13.8 (+331)	1.6 (+220)	10.5 (+228)	2.8 (+460)
Loam	16.5	0.3	28.8 (+74)	0.6 (+100)	83.3 (+405)	0.7 (+133)

* Figures in brackets denote percentage increases of treated soils with respect to controls.

the exception of the bacterial number on the sandy soil, *Durvillea* had a greater stimulatory effect on the soil micro-organisms than *Pachymenia* which is in agreement with the oxygen uptake data.

DISCUSSION

Glasshouse trials showed that *Pachymenia* meal did not affect the available soil nitrogen so as to limit plant growth while *Durvillea* must have immobilised it considerably as its inhibitory effect could be reversed by adding ammonium nitrate to the soil. An induced nitrogen deficiency, however, was probably not the only detrimental effect of *Durvillea* as pea plants which failed to show any signs of nitrogen starvation were slightly but significantly depressed in growth by the seaweed.

On comparing the soil-nitrogen and oxygen-uptake data and micro-organism counts, it becomes clear why plants grown on *Durvillea*-treated soils showed symptoms of nitrogen deficiency. In fact, it is surprising why this did not take place on soils treated with *Pachymenia*; these laboratory studies, however, were carried out under carefully controlled conditions of soil moisture, temperature and aeration and may therefore not give a complete indication of what happened in potted soils in the glasshouse.

Most previous workers have merely considered the removal of available nitrogen by soil micro-organisms as a function of the C/N ratio of the organic matter added. If only this is considered,

however, it would be difficult to explain the diversity in behaviour of the different soils studied when the same seaweed materials were added to all. Probably the amount of inorganic nitrogen removed from a soil after the addition of organic matter may also be dependent on other factors such as:

(1) The kind of micro-organisms stimulated. Jensen [4], for example, found that on an alkaline soil to which organic matter of a C/N ratio greater than 26 was added, no nitrification took place within 6 months. On an acid soil, however, he found the limiting ratio to be between 13 and 18. He concluded that this was due to the fact that in acid conditions fungi are relatively more active than bacteria, and it is known that they have a greater requirement for nitrogen when assimilating a given amount of carbon. The type of soil population will also depend on factors such as the kind of carbohydrates, proteins, and other compounds it contains, and on environmental conditions such as temperature and moisture of the soil.

(2) The C/N ratio of the soil is almost certainly a factor which plays a part in governing the equilibrium between the formation and release of available nitrogen by micro-organisms. Soils with ratios of about 10 are usually regarded as well balanced; when, however, this ratio is exceeded, the soil is considered to be deficient in nitrogen for optimum plant growth.

(3) The decomposition rate of the organic matter will govern the amount of inorganic nitrogen taken up by micro-organisms. This in turn will depend on the chemical composition of the material and climatic factors within the soil.

In the case of both the seaweeds it has been shown that the removal of inorganic nitrogen was very much more pronounced from the organic soil than from the loam, and this may be explained on the basis of the lower pH and higher C/N ratio of the organic soil. The higher microbiological activity of the loam, however, possibly helped to offset this difference in the relative amounts of inorganic nitrogen removed. The slower and less pronounced changes in the nitrogen metabolism of the sand were probably due to the relatively low micro-organism numbers present in this soil.

SUMMARY

The effects of applying dry meals from the seaweeds *Pachymenia himantophora* and *Durvillea antarctica* on the inorganic nitrogen metabolism and microbiological activity of soils has been investigated. Glasshouse trials have shown that plants grown on *Durvillea*-treated soil suffer from nitrogen deficiency which can be reversed by the addition of ammonium nitrate. Both the seaweeds, and in particular *Durvillea*, were found to immobilise inorganic nitrogen in soils. This removal of available nitrogen is considered to be due to the greatly stimulated microbiological activity shown to take place following seaweed treatment.

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THE EFFECTS OF SOIL ACIDITY ON THE GROWTH OF CEREALS WITH PARTICULAR REFERENCE TO THE DIFFERENTIAL REACTION OF VARIETIES THERETO

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INTRODUCTION

While the effect of lime deficiency on crop response and yield is well known, the exact mechanism by which plant growth becomes restricted in acid soils is less well understood. Gallagher [8] and more recently Hewitt [10], have pointed out that soil acidity is in fact a complex of a number of factors, the more important of which are toxicity of aluminium, manganese, or other heavy metals, and/or a deficiency of calcium, magnesium or molybdenum. The problem is further complicated by the fact that, not only do these elements act independently but also in some instances react with one another. For example, in studies by Walsh and Neenan [13], it was found that in an experiment where manganese toxicity was induced in swede turnips, phosphorus and to a lesser extent molybdenum interacted with manganese, resulting in a lowering of the concentration of this element in the foliage and an increase in yield of the crop. In the same experiment, although the application of aluminium salts increased both the water-soluble and the "available" aluminium content of the soil, the toxic effects of excess quantities of this metal were apparent only at low levels of phosphorus. In field experiments on the growing of cereals on lime-deficient soils it was found [2] that, while the drilling of ground limestone afforded no protection against the effects of acidity, a reasonably good crop could be obtained from the combine drilling of a moderate dressing of superphosphate. It was considered that

this effect could operate in two ways, either by the interactions of phosphorus with manganese in a manner similar to that indicated elsewhere [18] or alternatively by the precipitation of aluminium.

In peatland however, an intense chlorosis usually associated with iron-deficiency symptoms can be completely overcome by liming. It is thought that this may be due to the effects of lime in suppressing the availability of heavy metals other than manganese and aluminium.

That the toxicity of any element can be best defined in terms of the crop which is being grown, is apparent from the work of Hewitt [10], who found that while some species of plants were readily injured by aluminium, others were more sensitive to high levels of manganese, and *vice versa*.

Because of their diverse geological origin and of the operation of weathering factors at different levels of intensity, it is to be expected that individual soils would show marked differences in the levels of heavy metals which they would ultimately contain. For this reason, it is understandable that a particular crop might thrive in one acid soil but not in another. This has frequently been observed in Ireland; for example in one soil of pH 5.2 barley is a complete failure, while in neighbouring soil with the same level of acidity, excellent crops are obtained, and no increases in yield are obtained from liming. This is presumably due to the absence from the latter soil of elements which are toxic to barley.

Even plants whose genetic differences are so slight that they can only be designated varieties of the same species, show marked differences in their reaction to acid soils. Certain varieties of wheat have from time immemorial been grown on acid soils, while other varieties under the same conditions are known to be complete failures.

In Ireland, due to the fact that some 60 per cent of the land is deficient in lime to some degree [19], and also due to the greatly increased consumption of ground limestone in recent years, the reaction of individual crops and varieties to soil acidity has been receiving considerable attention.

EXPERIMENTAL

PRELIMINARY EXPERIMENT

In 1947, a rotational experiment with different forms of lime was laid down at Johnstown Castle. The soil was sandy loam derived from Silurian

shales and Quartzite and had an initial pH of 4.8. During the 1949 season, the individual liming treatments were split and sown to four varieties of wheat and four of barley [1].

Results

In the early stages of the experiment the wheat and barley plants on all the control plots showed tip withering followed by a purpling of the stems and leaf sheaths. At harvest time, the unlimed wheat was stunted, being about six inches shorter than the limed. As indicated elsewhere [1], the latter plots gave more than twice the yield of the former.

In analysing the results, however, it was observed that marked differences occurred between the varieties in the control plots on the different blocks, particularly so in Block II. In the limed treatments all yields were, (with the exception of the variety Karn which suffered from poor germination), approximately the same. This is apparent from the following table.

TABLE 1

Variety	Yields of grain in cwts per acre					
	Block I		Block II		Block III	
	Limed	Unlimed	Limed	Unlimed	Limed	Unlimed
Fylgia	37.1	28.0	40.9	16.5	47.1	33.0
Brons	39.5	25.0	39.5	16.2	43.9	31.2
Ella	43.6	24.5	44.8	7.1	44.8	26.8
Karn	26.5	15.9	27.1	1.5	32.4	16.5

It will be seen from this table that, in the unlimed plots of Block II, the varieties Brons and Fylgia gave yields of approximately 60 per cent, Ella gave 28 per cent, and Karn only 9 per cent of that obtained in Blocks I and III. This indicates that some acidity factors were present in Block II to which Karn and Ella were much more sensitive than the other two varieties. An examination of the site showed that Block II was situated in a slightly wetter area and was more subject to reducing conditions than were Blocks I and III. An analysis carried out when the soil was dried normally in the laboratory, revealed no great differences between the blocks. A similar analysis carried out when the moisture was at field capacity showed that the available manganese in Block II was in the regions of 100 ppm as against about 45 ppm for Blocks I and III.

RESPONSE OF WHEAT, BARLEY AND OATS TO THE APPLICATION OF MANGANESE UNDER FIELD CONDITIONS

Field experiment

During 1948, a field experiment was laid down at the same location and on the same soil type as the foregoing. The treatments consisted of manganese sulphate at 56 and 224 lbs, and aluminium sulphate at 56 and 400 lbs per acre, both applied separately. The experiment was in the form of a randomised block with four replications on two of which ground limestone was applied at three tons per acre. Each treatment was sown to wheat var. Atle, barley var. Spratt Archer 37/3, and oats var. Glasnevin Success 10. A basal dressing of N, P, K was given in the form of sulphate of ammonia, superphosphate and muriate of potash.

Results

In the presence of lime, there were little or no ill effects on any crop at the higher levels of manganese and aluminium. In the absence of lime, barley and wheat both showed typical symptoms of acidity, but oats remained unaffected. At the lower levels of manganese, there was somewhat of a reduction in vigour as compared to the control, barley being more severely affected than wheat. At the high level of manganese, there was a stunting effect accompanied by a black spotting over the leaf blade, as well as some tip withering.

The higher levels of aluminium produced a very severe stunting effect similar to that caused by acute phosphate deficiency. There was also severe tip withering, more pronounced in barley than in wheat.

Since the trial was primarily intended to verify by various means of visual symptoms, the causes of injury to plants on acid soils, yields were not taken in this experiment.

THE RESPONSE OF FOUR VARIETIES OF WHEAT TO DIFFERENT INCREMENTS OF LIME ON AN ACID SOIL

Pot experiment

In this experiment, four varieties of wheat known under field conditions to show a differential response to liming were chosen; Atle and Karn were selected as varieties very sensitive to lime deficiency, Progress less sensitive, April Red highly tolerant, and at that time widely grown in lime-deficiency areas. These were grown in pots in a light to medium acid,

brown loam derived from a mixture of Silurian and Granitic drift; this in its natural state had a pH of approximately 5.0. Under field conditions this had given a spectacular response to liming. Analysis showed it to be moderately high in readily soluble manganese. The soil without dilution was placed in 9″ earthenware pots treated with bitumastic paint. Each pot was treated as a separate unit, and received a basal dressing N, P, and K. The treatments consisted of CaO applied at the rate of 0, 1.25, 2.5, 10.0, 12.5, 17.5, and 20.0 gr. per pot; each treatment was replicated four times. The pots were kept in the open, and watered as required. Frequent observations were made on growth response.

Crop response

From an early stage there was distinct varietal response to liming. At the lower levels of liming, Progress and April Red showed most vigour and Atle the least. As between the different treatments April Red showed least response. At the end of the growing season the total overground produce of each pot was harvested and dried. Fig. 1 shows the yields of grain and straw obtained and also the effect of the different increments of lime,

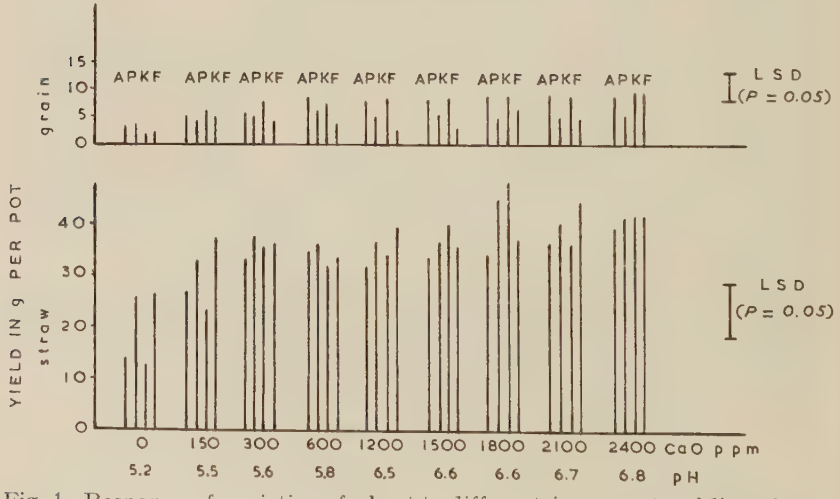

Fig. 1. Response of varieties of wheat to different increments of lime (ppm wt/wt soil) on an acid soil. A = Atle, P = Progress, K = Karn, F = April Red.

(quoted as ppm by weight), on the pH of the soil. For the latter analysis, the samples were taken at harvest time. Apart from differences in yield, the effects of acidity were also reflected both in the degree of tillering and in the plumpness of the grain; at the

TABLE 2

Chemical composition of varieties with different increments of lime. Results on a dry matter basis

Grams CaO per pot	Ca % A	Ca % P	Ca % K	Ca % F	P % A	P % P	P % K	P % F	K % A	K % P	K % K	K % F	Mg % A	Mg % P	Mg % K	Mg % F	Mn ppm A	Mn ppm P	Mn ppm K	Mn ppm F	Al ppm A	Al ppm P	Al ppm K	Al ppm F	Mo ppm A	Mo ppm P	Mo ppm K	Mo ppm F
0	.30	.20	.18	.28	.13	.11	.08	.09	1.2	.98	.89	1.2	.04	.03	.09	.04	104	86	100	128	66	63.5	43	34	.25	.25	.20	.20
1.25	.27	.20	.20	.35	.09	.12	.09	.07	.9	1.1	1.0	.95	.03	.05	.09	.06	86	98	72	114	33	30	24	41	.30	.20	.20	.20
2.5	.30	.23	.20	.28	.09	.12	.09	.10	.9	1.2	.76	1.2	.03	.05	.09	.06	68	82	104	72	26	25.5	25.5	28	.25	.25	.25	.24
5.0	.32	.27	.30	.32	.10	.10	.09	.09	.9	.87	.95	1.1	.05	.08	.10	.05	60	74	104	72	21	21	25.5	26	.20	.35	.20	.25
10.0	.28	.25	.30	.35	.10	.11	.09	.07	1.1	1.0	.85	.87	.04	.08	.10	.05	50	64	80	50	19	25.5	22	19	.40	.35	.25	.25
12.5	.30	.25	.25	.21	.09	.12	.08	.10	.95	1.1	.90	.98	.05	.09	.10	.05	41	72	80	66	16.5	23.5	17.5	14.5	.13	.45	.20	.35
15.0	.35	.25	.30	.30	.09	.12	.12	.10	.95	1.0	1.1	1.1	0.5	.08	.12	.05	46	54	68	44	10	20	19.0	18.5	.13	.35	.30	.45
17.5	.37	.32	.35	.30	.09	.10	.09	.07	.95	1.1	.95	.97	.08	.08	.11	.04	40	46	75	40	18	17.5	14.0	20.0	.35	.60	.30	.30
20.0	.36	.34	.35	—	.09	.10	.07	—	.90	1.2	.75		.06	.09	.09	—	40	61	64	—	8.5	11.5	16.5	—	.50	.65	.25	—

lower increments of lime the seed produced was shrivelled and contained very little endosperm. It is important therefore, to bear in mind that, apart from the effect on yield, acidity has also an important bearing on the quality of the grain produced.

In terms of total yield, April Red showed no significant increase above pH 5.5, Atle no increase above pH 5.8, whereas Karn showed a marked response to liming between pH 5.6 and 6.6. The variety Progress, while it outyielded Atle by a very considerable margin at the lower pH levels, attained maximum production at pH 6.6.

In order to obtain more specific information on the modes of interaction of the varieties with the soil, a chemical analysis of the leaf and stem tissue was carried out by the methods below.

Chemical analysis

Samples were wet ashed using nitric, sulphuric, and perchloric acids as described by Piper [16]. Calcium and potassium were determined in a DU Beckmann flame photometer. The other elements were determined colorometrically: – phosphorus by the ammonium molybdate method; magnesium by the brilliant yellow method [13]; aluminium by the A.O.A.C. method [3]; molybdenum by the dithiol method [16]; manganese by the sodium bismuthate method.

The results which are given in Table 2 show, with few exceptions, little difference between the varieties in respect of their content of calcium, phosphorus, potassium, and magnesium. In the case of aluminium and manganese however, there were marked differences not only between the different liming treatments but also in some instances between the varieties themselves. To bring this point out more clearly, and also in order to narrow the scope of the subsequent investigations, correlation coefficients were calculated between the yield and the concentration in the plant of a number of chemical elements. The results are set out in Table 3.

In the foregoing table, it will be seen that the correlation of yield and aluminium content is highly significant in the case of Atle and Progress, slightly less so in Karn and not significant for April Red. On the other hand, only Atle shows a significant correlation with manganese content. Karn shows a significant correlation with calcium content, whereas all varieties, Progress excepted, are significantly correlated with pH of the soil. The

TABLE 3

Correlation between yield and mineral content of the varieties at different levels of lime

Variety	Ca	P	K	Mg	Mn	Al	Mo	pH
Atle (A)	.5292	−.8359	−.7463	.4883	−.9063	−.9673	.1967	.7741
Prog. (P)	.5183	−.3131	.1043	.0801	−.3720	−.9458	.5489	.6496
Karn (K)	.6744	.2924	.0098	.5546	−.5672	−.8853	.6275	.8410
April Red (F)	.1075	−.1983	−.4494	.2397	−.6866	−.5656	.5608	.7353

For A, P, K, significant point is 0.6664 for $P = 0.05$
,, ,, ,, 0.7977 ,, $P = 0.01$
For F, significant point is 0.7067 for $P = 0.05$
,, ,, ,, 0.8343 ,, $P = 0.01$

correlations with P and K obtained with Atle are probably fortuitous since the analysis in Table 2 shows that the difference in K and P content are confined to a few levels which coincide with fairly large increases in yield. Although molybdenum deficiency has not so far been recorded in wheat in this country, it will be observed that in Table 3, the correlation coefficients between this element and yield approach the significant level in the case of three varieties. With a more sensitive method of analyses (Table 4) the differences in Mo-content are even greater than those quoted above. The amount of material harvested did not however permit of a spectrographic analysis of all samples.

Because of the possibility that other heavy metals might be involved, some plant material from contrasting treatments was subjected to a spectrographic analysis. This was carried out according to the procedure of Mitchell[14]. The results which are

TABLE 4

Spectrographic analysis of the varieties at the high and low levels of lime. Results in ppm of dry matter

Variety	Treatment	Nickel	Lead	Tin	Titanium	Vanadium	Molybdenum
Atle	High lime	0.58	1.1	0.41	6.2	0.15	0.58
	Low lime	0.88	1.6	0.21	6.6	0.16	0.13
Progress	High lime	0.42	1.14	0.13	8.5	0.10	0.40
	Low lime	1.06	1.3	0.21	5.9	0.20	0.14
Karn	High lime	0.82	0.80	0.18	7.5	0.19	0.51
	Low lime	0.95	0.77	0.16	11.7	0.30	0.20
April Red	High lime	2.10	9.4	0.20	16.0	0.31	1.16
	Low lime	1.53	2.16	0.47	13.2	0.35	0.26

given in Table 4 show that the levels of such elements as nickel and lead are within the normal range for plants of this type [12] and hence that the main effects must be due to the high levels of aluminium and manganese or possibly a deficiency of molybdenum.

The position therefore, is seen to be a complex one involving the differential reaction of varieties to manganese, aluminium, calcium and possibly molybdenum. In these experiments it has not been possible to study interactions between elements, but in view of previous findings it is likely that such may occur, and play an important part in the reaction of plants to acid soils. In order to obtain a better separation of the more important factors of the acidity complex, it was decided to undertake more critical experiments in sand culture.

SAND-CULTURE EXPERIMENTS ON THE SUSCEPTIBILITY OF DIFFERENT VARIETIES OF CEREALS TO ALUMINIUM AND MANGANESE TOXICITY

Experiment no. 1

Four varieties of wheat (Atle, Progress, Karn and April Red), two varieties of barley, Spratt Archer and Ymer, and four varieties of oats, were grown in 9″ pots in a medium of high-grade silica sand. A nutrient solution similar to that used by Hewitt [11], was applied twice weekly. Two levels of aluminium (18 and 36 ppm), and two equivalent levels of manganese (27.5 and 55 ppm), were applied also twice weekly, alternatively with the general nutrient solution, the control series receiving an equal quantity of distilled water at the same time.

Observations in the early growth stages showed no difference between the different treatments. Consequently, it was decided to alter the experiment by increasing the lower levels of aluminium and manganese to 54 and 82 ppm, respectively. Shortly afterwards, the variety Atle developed symptoms of both aluminium and manganese toxicity; Progress although unaffected by manganese showed symptoms of toxicity at both levels of aluminium. Karn and April Red, although showing some symptoms of aluminium toxicity were much less affected than the two aforementioned varieties. The effect of manganese on the yield was not appreciable except in the case of the variety Spratt-Archer, where there was a depression which was almost significant at the 5% point.

It is interesting to record however, that some of the oat varieties showed a response to the lower increments of manganese, and

that for one variety (Star), this was significant at the 5% level. Only the wheat variety Progress, which gave a significant decrease at the higher rate of application, showed any reaction to aluminium.

It can be seen therefore, that, at the levels used in this experiment, barley was more susceptible to injury from manganese than from aluminium, while in the case of wheat, the position was reversed. More important still was the fact that, as foreshadowed in Table 3, individual varieties behaved differently in regard to injury by these two elements.

Experiment no. 2

As it was felt that the levels of aluminium and manganese, employed in previous experiments were not sufficiently high to give full play to the interaction between varieties and these elements, it was decided to carry out further pot-culture experiments using the same four strains of wheat.

This experiment was carried out on the same general lines as the foregoing except that the first application of nutrient solution, to which aluminium and manganese had been added, was given immediately the seedlings emerged, and thereafter at twice weekly intervals. The treatments which were replicated four times, were as follows:

Aluminium: 0, 108, 162, 216, 270 ppm
Manganese: 0*, 27, 55, 82, 110, 137 ppm

Observations were made throughout the growing season and the plants were harvested at earing time. The differential response in this experiment is clearly shown in Plate 1; the yields are recorded in Fig. 2. Throughout the growing season very clear-cut differences were shown. Progress was affected most by aluminium toxicity followed by Karn and Atle, with April Red the least susceptible. The latter effect was particularly well shown at the 162-ppm level of aluminium. The general symptoms of aluminium toxicity were shown as lack of tillering, the development of a purplish colour on the lower leaves followed by severe tip withering and general stunting of growth. For manganese, little injury was shown by any of the varieties up to the 82-ppm level. At this level, Atle showed very definite signs of injury in the form of brown specks

* This means that no manganese was added other than that in Hewitt's [11] ordinary nutrient solution.

usually 2 to 3 millimetres in length running parallel to the veins, and in general covering the surface of the leaf. Karn was affected in a manner almost similar to Atle, while Progress was not so severely affected, while at this level April Red was unaffected. At the 110-ppm level while Atle was severely affected and Karn

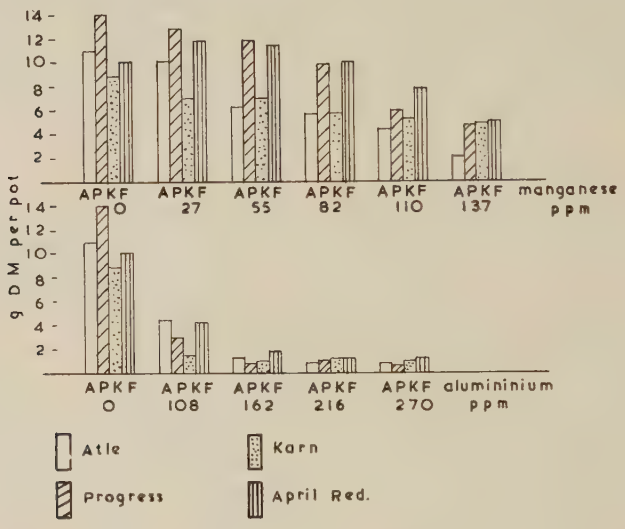

Fig. 2. Yield of varieties at different levels of manganese and aluminium.

almost equally so, April Red was but slightly affected as reflected in some tip withering, while Progress was much less affected than either Atle or Karn. At the highest level the difference between Progress and Atle was very outstanding, with Atle plants almost completely chlorotic, and Progress showing a reasonable amount of healthy growth. April Red showed reasonably good growth at this level of manganese also. These differences are adequately reflected in the yield results. They substantiate the previous findings, that, while Progress was tolerant of manganese toxicity it was susceptible to aluminium toxicity.

It will be noted that in this latter experiment, the varieties have tolerated much higher levels of manganese than in the experiments carried out in soil culture. The reason for this is not entirely obvious, but it would seem as though some factor other than manganese and aluminium, *e.g.* molybdenum deficiency was also operating, in the case of the earlier experiments.

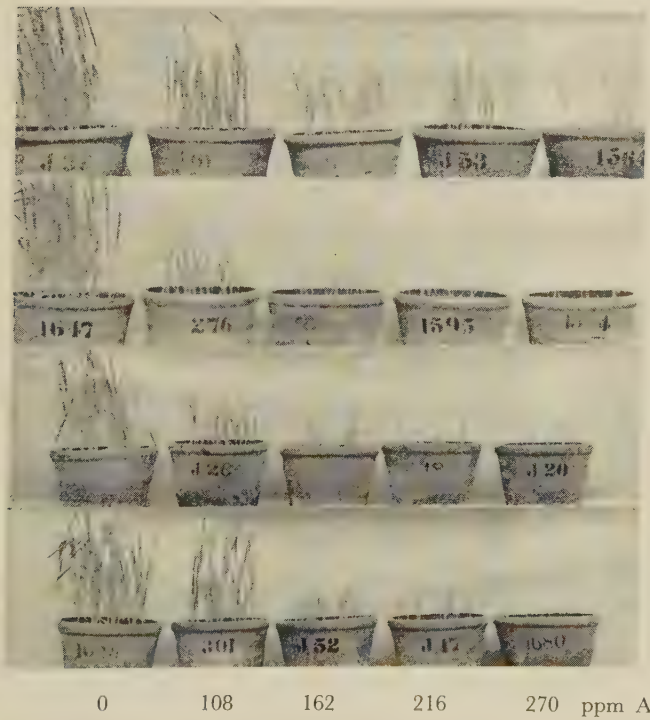

Plate 1. Effect of different concentrations of manganese and aluminium in solution on growth of different varieties of wheat.

GENERAL DISCUSSION

Although it has long been known in a general way that plants of different genetical constitutions show a differential reaction to soil conditions, hitherto no attempt has been made to explain the mechanisms by which this equilibrium between plant and soil is effected.

It has now been established that, not only species but even varieties, differ in their reaction to the individual factors which constitute the soil acidity complex. This is all the more surprising, in view of the very slight morphological differences which occur, and which presumably imply rather narrow genetic differences between such varieties. An analysis of the tissue however, (Figs. 3 and 4) shows that while at intermediate levels some differences in manganese content between the varieties may be observed, that at the higher applications of this element, all varieties contain about the same levels, *i.e.* 3,000–4,000 ppm of Mn. This would seem to suggest that the adaptability of certain of these varieties to strongly acid conditions is due, not so much to some ability on

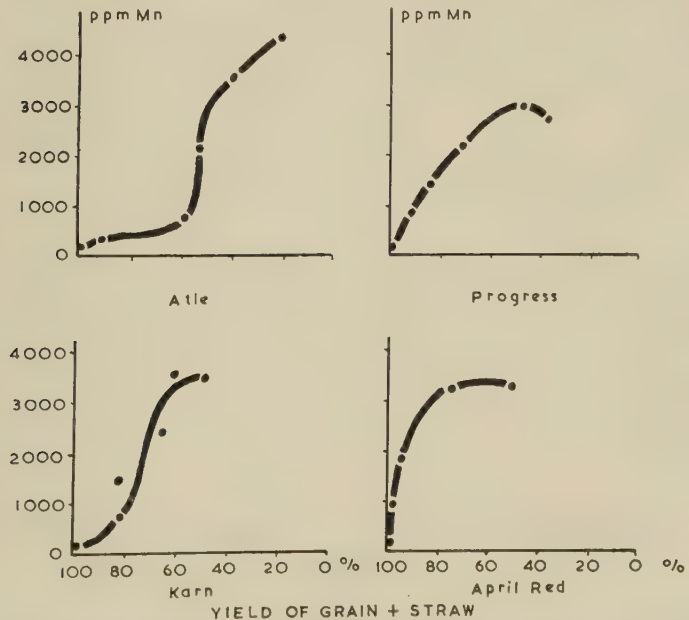

Fig. 3. Relationship between yield (grain + straw) and manganese content (ppm) of tops in sand-culture experiment.

their part to prevent the uptake of elements in toxic proportions, but rather to tolerate high levels of these substances and still maintain good growth. In previous experiments by Gallagher and Walsh [9] and the author [15], it was found that the variety Atle was highly sensitive and the variety April Red highly resistant to manganese deficiency. Hence it would appear that those varieties which can adapt themselves to different soils must possess some ability by which they can tolerate wide variations in their mineral composition, and still maintain good growth.

In this regard the work of Brown and his associates at Beltsville [4 5], would appear to be particularly revelant. These workers have produced conclusive evidence to the effect that the ability of certain species or varieties of plants to withstand mineral deficiencies may be explained on the basis of their enzyme systems. Plants which show symptoms of iron but not of copper deficiency all exhibited a low catalase activity, while other plants *e.g.* wheat, in which the terminal oxidase is believed to be ascorbic acid

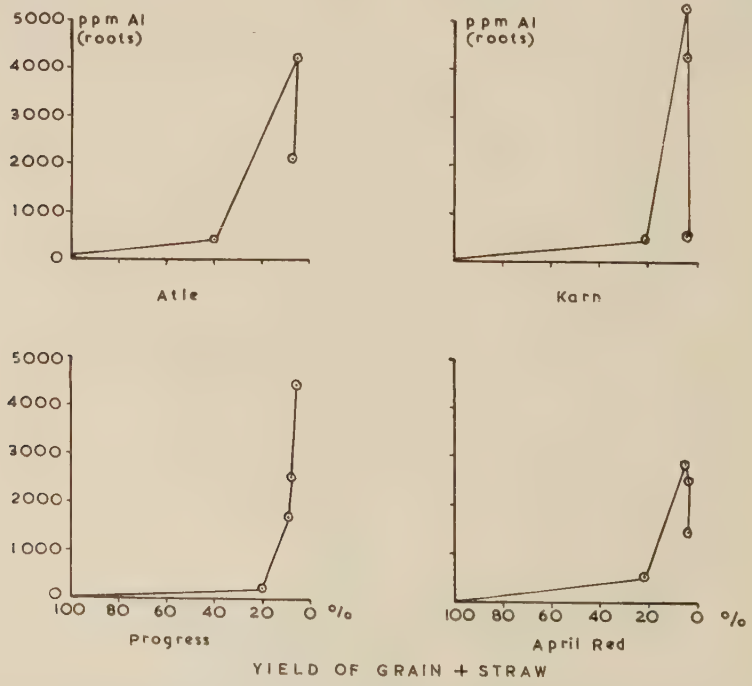

Fig. 4. Relationship between yield (grain + straw) and aluminium content (ppm) of roots.

oxidase, was highly susceptible to copper but, not to iron deficiency. In experiments with tobacco [6], it was found that the activity of these enzymes was also affected by deficiencies of manganese, molybdenum, boron, and zinc.

It now being generally accepted that plant enzymes are produced from the nucleoproteins in the nucleus of the cell, the connection between the adaptability of varieties and the genes or factors of heredity becomes immediately obvious.

Further studies in this sphere should be of considerable practical benefit, both from the point of view of breeding plants for particular environments, and of providing a more systematic and inexpensive method of testing new varieties.

SUMMARY

Although the cereals wheat and barley are normally regarded as sensitive to the effects of soil acidity, all varieties of these are not equally so. Some of the ways in which varieties react with soil acidity have been investigated. It was found that some varieties were tolerant of high aluminium, whereas others were tolerant of high concentrations of manganese. Because of their geological origin, individual soils show differences in the factors which cause injury to plants at low pH levels. It is suggested that this provides an explanation of the fact that some varieties of cereals will thrive on one acid soil but not in another. The application of this principle to plant breeding is discussed.

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EFFECT OF MAGNESIUM AND CALCIUM SUPPLY ON THE UPTAKE OF MANGANESE BY VARIOUS CROP PLANTS *

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1. Introduction.

2. Experimental methods.
   a. Preliminary observations.
   b. Field experiments.
   c. Solution culture experiments.
   d. Chemical methods.

3. Results and discussions.
   a. *Phaseolus vulgaris.* Var. Bruine boon.
   b. *Phaseolus vulgaris.* Snapbean (var. Dubbele Prinsesseboon).
   c. *Medicago sativa.*
   d. *Brassica napus* (var. Zomerkoolzaad).
   e. *Glycine hispida.*
   f. *Cichorium intybus.*
   g. Oats (var. Adelaar).
   h. Wheat (var. van Hoek's zomertarwe).
   i. Rye (var. Petkuser zomerrogge).
   j. Barley (var. Kenia zomergerst).
   k. Flax (var. Concurrent).
   l. Mangold (var. Groenkraag).
   m. *Lupinus luteus* and *Ornithopus sativus.*

4. General discussion.

5. Summary.

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* Up to 1958 this investigation was carried out under the National Council for Agricultural Research T.N.O. (Applied Scientific Research).

1. INTRODUCTION

The fact that magnesium may reduce the uptake of toxic amounts of manganese has been briefly reported by the author [16]. For potatoes this phenomenon has been investigated in more detail [15]. Data gathered for other crop plants will be presented below along with data for a similar property of calcium.

2. EXPERIMENTAL METHODS

a. *Preliminary observations*

For a number of years the effect of toxic amounts of manganese has been studied by the author in the experimental plots in the garden of the Laboratory of Microbiology at Wageningen [13] [14]. A triplicate series of 6 plots (each plot 42 m^2) was laid out in 1922 and each plot supplied with different amounts of ground limestone (0–10–15–30–60 kg). Two further plots in duplicate received either ammonium sulphate or chilean nitrate as nitrogen fertilizers. Except as to nitrogen in the latter, all the plots received a similar manurial treatment and were in each year planted with the same crops which varied from year to year.

After 1940 half of each plot was each year planted with potatoes but since 1949 this has been reduced to one third. On the remaining parts of the plots various crops were tested for sensitivity to an excess of manganese. Each year *Phaseolus vulgaris* (var. Bruine boon) and snapbean (var. Dubbele Prinsesseboon) were included, because they are most prone to injury from excess of manganese.

War conditions made potassium sulphate ('patentkali') with its additional amount of magnesium unavailable during many years. In 1944 oats was grown on the no-limestone and on the ammonium sulphate plots as a test for the occurrence of magnesium deficiency. No deficiency signs were observed. Since 1948, however, potatoes have shown severe signs of magnesium deficiency. In 1949 at the beginning of June these symptoms were very conspicuous and a topdressing of $MgSO_4$ at the rate of 170 kg per ha was applied to the potatoes and the adjoining row of beans (Bruine boon) in half of each of the unlimed and ammonium sulphate plots. The magnesium was supplied too late to have any visible favorable influence on the potatoes, but in the adjoining row of beans a curious effect was noted. Although at the moment of magnesium dressing the manganese injury was very obvious in the young bean plants, a few weeks later an unexpected difference between both half-plots could be seen. The bean plants treated with Mg had developed fairly well, although they still showed symptoms of injury by manganese excess in the older leaves, but the plants without additional magnesium had remained dwarfed and showed the well-known signs of severe Mn-injury. When the content of Mn was estimated in the leaves, that in

the plants receiving Mg proved much lower than in the plants lacking Mg, *viz* in ppm of plant material:

Unlimed plot	+Mg	0-Mg
I	1823	2614
II	1553	2664

Some data were collected on the amount of exchangeable manganese in the soil from the corresponding half-plots, but the exchangeable manganese in the plots lacking Mg did not exceed the amount in the Mg-treated ones. So magnesium seemed to act depressingly on the uptake of manganese.

b. *Field experiments*

In the account the plots will be named according to their treatment as follows:

Treatment	Replicates		
Lime kg 0	I_0,	II_0,	III_0
,, ,, 5	I_5,	II_5,	III_5
,, ,, 10	I_{10},	II_{10},	III_{10}
,, ,, 15	I_{15},	II_{15},	III_{15}
,, ,, 30	I_{30},	II_{30},	III_{30}
,, ,, 60	I_{60},	II_{60},	III_{60}
Ammonium sulphate	ASI	ASII	

In the years following 1949 halves of all experimental plots were supplied with $MgSO_4$ (170 kg per ha), half-plots being termed 0-Mg and +Mg and the behaviour of a number of crop plants was compared on corresponding half-plots.

Initially the experimental field served this purpose very well, but in later years the injury due to excess of manganese diminished very much in the most acid crops. This may be partly explained by small applications of cow dung which had been supplied to these plots in 1953, because development of sensitive crops had been reduced to nearly total failure. Moreover plot I_0, where the injury had been highly conspicuous, had in 1953 become flooded by excessive rainfall and material from the surrounding gravelled soil had influenced the soil status. These facts do not explain however the general gradual decrease of Mn-injury which occurred also in the plots supplied with 5 or 10 kg limestone.

The amount of exchangeable Mn extracted by $\frac{1}{2}N$ $Ca(NO_3)_2$ solution was frequently estimated. In a former paper [14] it was pointed out, that these estimates may vary greatly in a single plot when sampled at various times in a same year, thus having only a relative value. Nevertheless in Fig. 1 where a range of amounts of exchangeable Mn in I_0, II_0 and III_0, I_5, II_5 and III_5, and ASI and ASII are taken up, a downward trend in the succeeding years is evident with only a rise in 1957.

More important, however, is the fact that the addition of magnesium

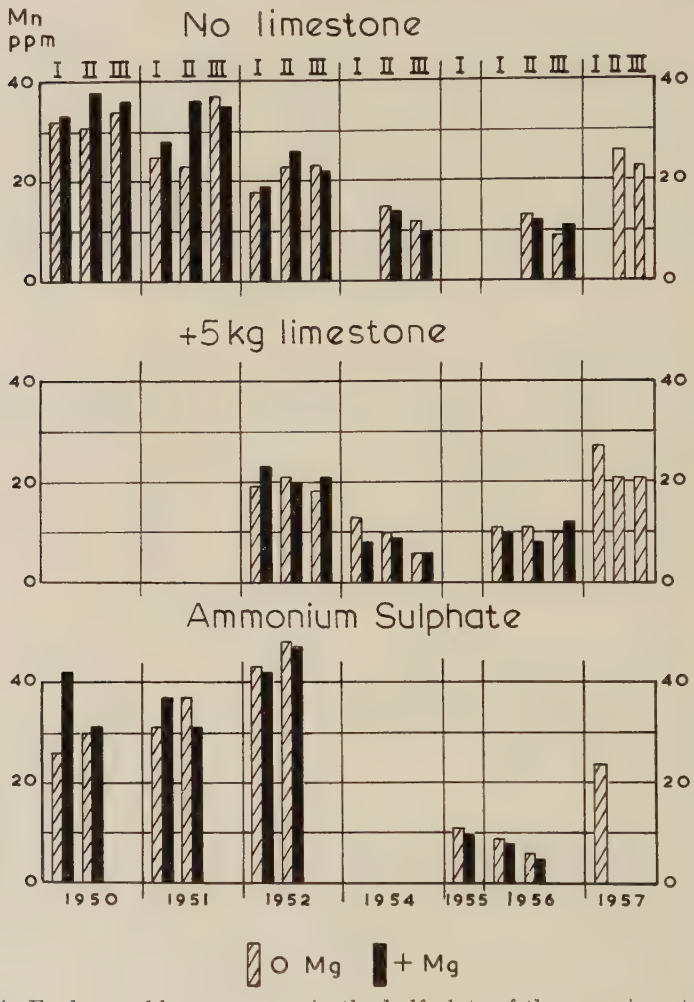

Fig. 1. Exchangeable manganese in the half-plots of the experimental field.

does not result in a decrease in exchangeable manganese as shown by a comparison of +Mg and 0-Mg plots. Thus the lower uptake of manganese by plants from +Mg half-plots cannot be explained by a lower availibility of manganese.

c. *Solution-culture experiments*

The action of Mg and Ca was tested in solution cultures. Various nutrient solutions were used. Initially modifications of Zinzadze pH 5 were used, as this solution had proved less prone to induce Mn-injury along with a

lower content of Mg than other culture solutions. It was not suitable, however, for modifications of the Ca-level, since a substitution of Na_2HPO_4 for $Ca_3(PO_4)_2$ appeared to act strongly on the solubility of Mn supplied as $MnSO_4$. Some crop plants developed better in Solution II. Von der Crone solution, low in Mg and Ca was very prone to induce Mn-injury. Modification of the Ca-level was obtained by substituting $Ca(NO_3)_2$ for KNO_3. In Nightingale solution [22] were Ca is soluble, its level could be easily modified.

All experiments were carried out in 1-litre glass vessels in which the plants (generally 4 in each) were supported in holes in plaster of paris lids. Experiments were generally run in triplicate.

The nutrient solutions used had the following composition:

Von der Crone solution, modified by Bryan.

KNO_3 1 g; $CaSO_4$ 0.2 g; $MgSO_4$ 0.2 g; $Ca_3(PO_4)_2$ 0.2 g; $FePO_4$ 0.2 g; 1 litre tapwater.

Zinzadze pH 5.

NH_4NO_3 0.334 g; KNO_3 0.166 g; $Ca_3(PO_4)_2$ 0.7 g; KCl 0.616 g; $MgSO_4$ 0.5 g; $CaSO_4$ 0.5 g; $Fe_2(SO_4)_3$ 0.25 g; 1 litre tapwater.

Zinzadze pH 5.5–6.5, modified, termed in the following as Solution II.

KNO_3 0.5 g; NH_4NO_3 0.2 g; $Ca_3(PO_4)_2$ 0.5 g; $MgSO_4$ 0.25 g; $Fe_2(NH_4)_2(SO_4).24H_2O$ 0.175 g; 1 litre tapwater.

Nightingale.

$Ca(NO_3)_2$ 2.12 g; KH_2PO_4 0.66 g; $MgSO_4$ 0.54 g; 1 litre tapwater.

Minor elements were added to all solutions in the following amounts per litre: H_3BO_3 0.5 mg; $CuSO_4$ 0.125 mg; $ZnSO_4$ 0.5 mg. As source of Mn, $MnSO_4$ was used.

In earlier experiments it had often proved difficult to prevent Fe-deficiency. Later the method described by Jacobson [11] in which sequestrene is used as an iron-chelating agent proved very satisfactory.

Whenever the composition of a solution was modified, another ion in equivalent amount was substituted for the one removed. In von der Crone solution K_2SO_4 was substituted for the KNO_3 omitted.

d. *Chemical methods*

For estimation of manganese the same method was used as in 1951, *viz* a colorimetric one with a Pulfrich photometer.

For estimation of magnesium in soil the Aspergillus method as worked out by Smit and Mulder [26] was utilized. (25γ Mg in 3 g soil will induce injury in barley, 150γ gives normal growth).

For estimation of Mg in plant samples the method of Deijs and Hekman* was used.

* A 1-g air-dried sample is ashed in an evaporating basin. The ash is twice evaporated

3. RESULTS AND DISCUSSIONS

a. *PHASEOLUS VULGARIS* (VAR. BRUINE BOON)

Field experiments

In 1951 the bean plants in the more acid 0-Mg half-plots showed distinct symptoms of Mg-deficiency. In young plants the primary leaves had taken on a brownish purple shade which could easily be seen at a distance. When the plants had further developed, the later leaves took on this same shade and appeared slightly crinkled. Such plants, however, continued to develop and when no injury by excess of Mn had set in, produced flowers and pods. On one and the same plant symptoms of Mg-deficiency in the basal part and of Mn-injury in the top might occur and could easily be recognized as such.

In 1952 young trifoliate leaves were sampled from plants where Mg-deficiency could be detected in the 0-Mg half-plots and Mn-injury in both parts (Plate 1A). Estimation of the content of Mn gave the following results (Table 1).

TABLE 1

Mn-content of plants in experimental plots			
Plot	Mn ppm		
	0-Mg	+Mg	Difference 0-Mg and +Mg
I	1175	542	+633
III_0	687	556	+131
ASI	2349	1392	+957

The 0-Mg samples surpassed the +Mg ones markedly in Mn-content.

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on a boiling water bath with 5 drops of HCl 25%. Then 8 drops of HCl are added and after 10 minutes the contents are rinsed into a measuring flask of 100 ml and filled up to mark. 5 ml of a filtrate thereof is pipetted into a measuring flask of 25 ml. Subsequently are added:

1. 5 ml *N* acetic acid.
2. 4 ml saccharose–starch solution (dissolve 3 g saccharose in 75 ml hot water in a 100 ml flask, add 2 g starch and fill up to mark).
3. 2 ml titan yellow solution (1 g/litre water).
4. 5 ml NaOH 4.5 *N* which contains 10 Fe/ml (180 g NaOH is dissolved in 750 ml water and 10 ml of a solution of 861 mg $Fe_2(NH_4)_2(SO_4)_4.24H_2O$ in 100 ml water is slowly added. The solution is then made up to 1 litre.
5. Fill up to 25 ml. The colour is measured photometrically and compared with Mg standard.

(Stencil, Centr. Inst. Landbouwk. Onderz., Wageningen).

Solution-culture experiments

An investigation of the action of different amounts of magnesium in von der Crone solution (normal 0.2 g $MgSO_4$) gave the following results (Table 2) *.

TABLE 2

Mn-content of plants in modified von der Crone solutions			
Mn ppm			
Solution	Solution	Plants	Difference from normal
$MgSO_4$ 0.4 g	10	1358	−108
$MgSO_4$ 0.2 g	10	**1466**	
$MgSO_4$ 0.1 g	10	1783	+317

Thus the antagonistic action of Mg on the uptake of Mn was demonstrated here.

b. SNAPBEANS. (VAR. DUBBELE PRINSESSEBOON)

Field experiments

It had been noted in earlier years that "Prinsesseboon" was more sensitive for Mn-injury than "Bruine boon", in fact among all the crop plants studied it was the most prone to show this injury. After the yearly fertilizing of each half-plot with magnesium had been started, each part was planted with at least one row of

TABLE 3

Mn-content (ppm) in snapbean plants from experimental plots						
Plot	Year	0-Mg		+ Mg		Diff. 0-Mg and + Mg
		Mn	Symptoms	Mn	Symptoms	
I_0	1952	1308	+++	972	+++	+ 336
I_0	1953	983	+	769	+	+ 214
II_0	1950	1068		765		+ 303
II_0	1953	688	+	588	+	+ 100
II_0	1956	367	+	203		+ 164
II_0	1957	277	+	170		+ 107
III_0	1950	2076	++++	576	++	+1400
III_0	1953	1269	+++	922	++	+ 347
III_0	1957	258	±	163		+ 95
ASI	1950	3419	++++	2322	++++	+1097
ASI	1953	2711	+++	2380	++++	+ 331
ASI	1956	367	++	303	+	+ 64
ASI	1957	865	+++	575	++	+ 290
I_5	1956	301	+	205		+ 96
I_5	1957	492	++	268		+ 224

* In the following tables the Mn-content of the unmodified solution is always in bold print.

snapbeans. Symptoms were recorded and corresponding samples from the acid plots were gathered and analyzed for manganese. Results are presented in Table 3.

In all samples the 0-Mg plants exceeded markedly the +Mg plants in Mn-content and were often more severely affected. As has been mentioned (p. 341) the visible injury decreased in course of time and this corresponded with a decrease in the Mn-content in samples of a same plot.

Solution-culture experiments

Initially the influence of Mg was studied and later also that of Ca. The first experiments were carried out in Zinzadze solution (Table 4).

TABLE 4

Mn-content in snapbean plants in modified Zinzadze solutions

Solution	Mn ppm			Mg ppm (plants)
	Solution	Plants	Diff. with normal	
1955 $MgSO_4$ 0.5 g	10	**604**		
$MgSO_4$ 0.125 g	10	928	+324	
$CaSO_4$ 0.125 g	10	887	+283	
1956 $MgSO_4$ 0.5 g	10	**443**		
$MgSO_4$ 0.25 g	10	472	+ 29	
$MgSO_4$ 0.125 g	10	550	+107	
$MgSO_4$ 0.06 g	10	759	+316	
1955 $MgSO_4$ 0,5 g	5	**272**		**1460**
$MgSO_4$ 0,125 g	5	272	0	—
$MgSO_4$ 0.06 g	5	250	− 22	880
$MgSO_4$ 0	5	374	+102	840
1956 $MgSO_4$ 0.5 g	5	**372**		
$MgSO_4$ 0.25 g	5	396	+ 69	
$MgSO_4$ 0.125 g	5	413	+ 86	
$MgSO_4$ 0.06 g	5	392	+ 65	
1955 $MgSO_4$ 0.5 g	2.5	**215**		
$MgSO_4$ 0.06 g	2.5	277	+ 62	
$MgSO_4$ 0	2.5	254	+ 39	

In the fourth column of this table an increasing trend in the uptake can be seen for all cultures. In 1955, 10 Mn, a reduction in supply of $CaSO_4$ has induced as well an increase in uptake of Mn. In 1955, 5 Mn, the amount of Mg in the harvested plants was

estimated and apparently diminished with a lowering of the supply. The fact that when no $MgSO_4$ had been supplied the content was still considerable, was mainly due to the use of tapwater.

Von der Crone solution. When 10 or 5 mg Mn were supplied changes in the composition were brought about by increasing the amount of $MgSO_4$ or by substituting $Ca(NO_3)_2$ for KNO_3 and supplying K as K_2SO_4. Two and a half mg Mn was too low to induce visible injury in the unmodified solution but when the supply of $MgSO_4$ was reduced, a slight injury was induced (Plate 1B).

TABLE 5

Mn-content in snapbean plants in modified von der Crone solutions

Solution	Mn ppm			Mg ppm in plants
	Solution	Plants	Diff. with normal	
1956 $MgSO_4$ 0.5 g	10	694	− 72	
$MgSO_4$ 0.2 g	10	**766**		
1957 $Ca(NO_3)_2$	10	1195	−355	
KNO_3	10	**1550**		
1956 $MgSO_4$ 0.5 g	5	419	− 54	
$MgSO_4$ 0.2 g	5	**473**		
1957 $MgSO_4$ 0.5 g	5	490	−193	
$MgSO_4$ 0.2 g	5	**683**		
$Ca(NO_3)_2$	5	471	−212	
1955 $MgSO_4$ 0.4 g	2.5	279	− 51	2040
$MgSO_4$ 0.2 g	2.5	**330**		1300
$MgSO_4$ 0	2.5	418	+ 88	1000
1956 $MgSO_4$ 0.4 g	2.5	153	− 99	
$MgSO_4$ 0.2 g	2.5	**252**		
$MgSO_4$ 0.05 g	2.5	285	+ 33	
1957 $MgSO_4$ 0.4 g	2.5	150	+ 3	
$MgSO_4$ 0.2 g	2.5	**147**		
$MgSO_4$ 0.025 g	2.5	244	+ 97	

In Table 5 the data for plants on von der Crone solution are recorded. For the cultures 1955, 2.5 Mn, the Mg-uptake of the plants was found to correspond in trend to the decrease of supply. Culture 1957, 5 Mn showed the marked depressing action of either Mg or Ca on the uptake of Mn. Here again the visible injury corresponded with differences in Mn-content of a similar range of plants.

Nightingale solution. As Ca is in soluble form, its level can be changed as easily as the Mg-level. Table 6 presents the results.

TABLE 6

Mn-content in plants in modified Nightingale solutions

Solution	Mn ppm		
	Solution	Plants	Diff. with normal
1956 Normal	10	**393**	
$^1/_8$ $MgSO_4$	10	393	0
$^1/_8$ $Ca(NO_3)_2$	10	529	+136
1957 Normal	10	**545**	
$^1/_8$ $MgSO_4$	10	607	+ 62
$^1/_{16}$ $MgSO_4$	10	670	+125
$^1/_8$ $Ca(NO_3)_2$	10	964	+419
$^1/_{16}$ $Ca(NO_3)_2$	10	1508	+963
1957 Normal	10	**922**	
$^1/_8$ $MgSO_4$, $^1/_8$ $Ca(NO_3)_2$	10	1902	+980
1958 Normal	10	**490**	
$^1/_{16}$ $MgSO_4$	10	546	+ 56
$^1/_{16}$ $Ca(NO_3)_2$	10	866	+376
$^1/_{16}$ $MgSO_4$, $^1/_{16}$ $Ca(NO_3)_2$	10	1040	+550

The experiments of 1957 and 1958 give evidence that a reduction in the Ca-concentration acts more strongly than a reduction of Mg, although the trend of action is the same. Here again the visible injury corresponds with the Mn estimated (Plate 1C).

c. MEDICAGO SATIVA

Field experiments

In 1951 the injury due to excess of Mn was described by the author [14] and very high contents of Mn in the affected plants were reported. In 1952, 1953, and 1957 lucerne was grown in the experimental plots with a view to studying the effect of differences in supply of Mg. The only plot wherein Mn-injury could be detected was ASI. Here in 1952 all plants were severely injured and dwarfed and the Mn-content was on a similar level to that reported in 1951, *viz* 0-Mg 2440 and +Mg 2405 ppm. In 1953 all the plants in this plot again remained small and in 1957 on the 0-Mg half-plot some injury occurred (Mn-content: 691), while on the +Mg part both

healthy and diseased plants were present. A sample of the former contained 202, of the latter 499 Mn ppm. Thus the experimental plots only furnished very slight evidence of a depressing effect of Mg on the uptake of Mn.

Solution-culture experiments

This question has been further studied by means of nutrient solutions.

TABLE 7

Mn-content of *Medicago sativa* plants in modified von der Crone solutions

Solution	Mn ppm		
	Solution	Plants	Diff. with normal
1956 $MgSO_4$ 0.2 g	10	**655**	
$MgSO_4$ 0.05 g	10	637	− 18
1957 $MgSO_4$ 0.5 g	10	922	0
$MgSO_4$ 0.2 g	10	**922**	
$Ca(NO_3)_2$ 1.18 g	10	572	−350
1955 $MgSO_4$ 0.2 g	5	**604**	
$MgSO_4$ 0.05 g	5	587	− 17
$MgSO_4$ 0	5	787	+183
1956 $MgSO_4$ 0.2 g	5	**452**	
$MgSO_4$ 0.05 g	5	524	+ 72
1956 $MgSO_4$ 0.2 g	2.5	**210**	
$MgSO_4$ 0.1 g	2.5	204	− 16
$MgSO_4$ 0.05 g	2.5	265	+ 55

Increasing the amount of Mg in the von der Crone solution did not influence the uptake of Mn (Table 7). Increasing the amount of Ca, however, induced a very marked reduction, while hardly any visible injury could be seen.

When the amount of Mg was reduced along with a normal supply of Mn (0.5 mg/l) signs of Mg-deficiency occurred. The older leaflets showed an intervenal chlorosis and eventually necrosis and the top margin became necrotic (cf Wallace [28], pl. 217). The symptoms could be clearly distinguished from those of excess of Mn.

TABLE 8

Mn-content of *Medigaco sativa* plants in modified Nightingale solutions

Solution	Mn ppm		
	Solution	Plants	Diff. with normal
1956 Normal	10	**359**	
$^1/_8$ $MgSO_4$	10	400	+ 41
$^1/_8$ $Ca(NO_3)_2$	10	943	+584
1956 Normal	10	**524**	
$^1/_8$ $MgSO_4$	10	537	+ 13
$^1/_8$ $Ca(NO_3)_2$	10	786	+262
1956 Normal	10	**707**	
$^1/_8$ $MgSO_4$	10	610	− 97
$^1/_8$ $Ca(NO_3)_2$	10	1394	+687
$^1/_{16}$ $MgSO_4$	10	550	−157
$^1/_{16}$ $Ca(NO_3)_2$	10	930	+223
1956 Normal	5	**249**	
$^1/_8$ $MgSO_4$	5	162	− 87
$^1/_8$ $Ca(NO_3)_2$	5	236	− 13
1957 Normal	5	**330**	
$^1/_8$ $MgSO_4$	5	237	− 93
$^1/_8$ $Ca(NO_3)_2$	5	355	+ 25
$^1/_{16}$ $MgSO_4$	5	225	−105
$^1/_{16}$ $Ca(NO_3)_2$	5	445	+115
1958 Normal	5	**308**	
$^1/_8$ $MgSO_4$	5	262	− 46
$^1/_8$ $Ca(NO_3)_2$	5	422	+114
$^1/_8$ $MgSO_4$, $^1/_8$ $Ca(NO_3)_2$	5	475	+167

Experiments in the Nightingale solution (Table 8) gave similar, but more clear-cut results. Lowering the level of Mg in the presence of normal Ca, did not increase the uptake of Mn. Lowering the Ca-level, however, influenced the uptake strongly. Evidently its action preponderated over the action of Mg.

d. BRASSICA NAPUS

Field experiments

In 1955 Middelburg drew my attention to a very severe injury in rape plants on a very acid soil, which might be due to Mn-excess. In 1957 he published a report of his experiments [17]. In this connection I took on rape (var. Zomerkoolzaad) as an

experimental crop and grew it in 1956 and 1957. As in these latter years the available Mn in the soil had decreased, injury could be detected only in the full-grown plants in some of the most acid plots, irrespective of the application of Mg. The injury occurred on the leaves of the flowering stems, their margins turning a pale white.

When samples were analysed from I_0 and II_0 plots positive as well as negative differences between 0-Mg and +Mg half-plots occurred. However in ASI in 1957 the samples from 0-Mg, where plants were affected, contained 628 ppm, while healthy plants from the +Mg half-plot contained 348 ppm, affected ones 517.

Solution-culture experiments

The results are shown in Table 9.

In von der Crone solution with 10 ppm Mn severe symptoms could be induced in young plants, *viz* a paling of the leaf beginning at the margin and finally reaching the middle nerve. Growth was stunted (Plate 1D).

TABLE 9

Effect of various nutrient solutions on the Mn-content of *Brassica napus*

Nutrient solution	Mn ppm		Symptoms
	Solution	Plants	
von der Crone	10	1843	very severe
	5	675	margins pale
	2.5	390	growth restricted
	0.5	—	healthy
Nightingale	10	644	margins pale
	5	524	narrow pale margins

The influence of Mg and Ca on the uptake of Mn was studied in solution cultures (Table 10). As the uptake of Mn in von der Crone solution exceeded the uptake from the other solution, 5 ppm Mn was the highest concentration studied.

Apparently reduction in the supply of Mg brings about an increase in the Mn-uptake. Reducing Ca, however, does so to a much greater degree. Visible injury increased along with the content of Mn. Decrease of Mg or Ca in the presence of 0.5 ppm Mn did not induce any symptoms.

TABLE 10

Mn-content of *Brassica napus* plants in modified nutrient solutions				
Nutrient solution	Modification	Mp ppm		
		Solution	Plants	Diff. with normal
Zinzadze	$MgSO_4$ 0.5 g	10	**484**	
	$MgSO_4$ 0.125 g	10	707	+223
	$MgSO_4$ 0.06 g	10	962	+478
	$MgSO_4$ 0.5 g	5	**308**	
	$MgSO_4$ 0.125 g	5	367	+ 59
von der Crone	$MgSO_4$ 0.5 g	5	639	− 68
	$MgSO_4$ 0.2 g	5	**707**	
Nightingale	Normal	10	**583**	
	$^1/_8$ $MgSO_4$	10	841	+258
	$^1/_8$ $Ca(NO_3)_2$	10	1451	+868

e. GLYCINE HISPIDA

Field experiments

In 1951 and 1952 soya beans were grown on the experimental plots. In the acid plots plants were severely affected. They remained small, leaves were crinkled and cupped downward with dark specks on the margins. In the corresponding 0-Mg half-plots the margins of the leaves were often chlorotic and intervenal necrotic zones occurred. In the AS plots plants remained small on both half-plots and the plants showed a distinct curling and mottling of the top leaves (Plate 2A). In Table 11 the Mn-content of 0-Mg and +Mg plots are recorded.

Plate 1:

A. "Bruine boon" from unlimed plot (1952). *Left:* No Mg added. *Right:* +Mg.

B. Prinsesseboon in von der Crone solution, 1955. *From left to right:* 0 $MgSO_4$ − 0.5 mg Mn; 0 $MgSO_4$ − 2.5 mg Mn; 0.2 g $MgSO_4$ − 2.5 mg Mn; 0.4 g $MgSO_4$ − 2.5 g Mn.

C. Prinsesseboon in Nightingale solution, 10 mg Mn, 1958. *From left to right:* Normal; $^1/_{16}$ $MgSO_4$; $^1/_{16}$ $Ca(NO_3)_2$; $^1/_{16}$ $MgSO_4$, $^1/_{16}$ $Ca(NO_3)_2$.

D. *Brassica napus* in von der Crone solution. *From left to right:* 10 mg Mn; 5 mg Mn; 2.5 mg Mn; 0.5 mg Mn.

Plate 1

Plate 2

TABLE 11

Mn-content of *Glycine hispida* plants from experimental plots

Plot	Year	Mn ppm		
		0-Mg	+Mg	Diff. 0-Mg and +Mg
I_0	1951	1414	890	+ 524
I_0	1952	730	730	0
II_0	1951	694	488	+ 206
II_0	1952	1089	820	+ 269
III_0	1951	1069	634	+ 435
III_0	1952	1405	1122	+ 283
ASI	1951	2742	1407	+1335
ASI	1952	2705	2137	+ 568
ASII	1951	2208	1278	+ 930
ASII	1952	2008	1367	+ 641

Only in one unlimed plot were the Mn-contents in the +Mg and 0-Mg plants on the same level. Plants in this plot showed only the marginal chlorosis and no crinkling of the leaves.

Solution-culture experiment

The injury caused by excess of Mn could be reproduced by means of cultures in von der Crone solution. Ten ppm Mn induced a Mn-content in the plant of 765 ppm, and 5 ppm one of 295. The symptoms agreed with those of the unlimed plots. Mg-deficiency symptoms could be induced by omitting Mg in the solution, the intervenal zones growing dark and limp and later necrotic. In younger leaves these intervenal zones became yellow. In the 0-Mg plots similar spots were detected.

The injury noted in the acid plots can therefore be ascribed to an additive action of excess of Mn and Mg-deficiency for here the low supply of Mg would have augmented the uptake of Mn.

Plate 2:

A. *Glycine hispida* from AS plot. *Left:* No Mg added. *Right:* +Mg.

B. *Cichorium intybus*. *Left:* Unlimed. *Right:* 60 kg lime.

C. *Cichorium intybus* in von der Crone solution. *From left to right:* 0 $MgSO_4$ —20 mg Mn; 0.2 $MgSO_4$—20 mg Mn; 0 $MgSO_4$—0.5 mg Mn; 0.4 g $MgSO_4$—0.5 mg Mn.

D. *Cichorium intybus*. Von der Crone solution, 0 $MgSO_4$. *From left to right:* Tapwater, 0.5 mg Mn; dist.w., 0.5 mg Mn; dist.w., 20 mg Mn.

For this crop a corroboration of the latter action by means of solution cultures is lacking.

f. CICHORIUM INTYBUS

Field experiments

In connection with other problems *Cichorium intybus* was grown on the experimental plots in 1952, 1953, and 1955. Especially in the first year differences in lime supply induced very strong differences in development (Plate 2B). Plants on the unlimed plots remained small and sprightly, the leaves somewhat crinkled often with reddish purple specks on the main nerve and necrotic edges. In 0- and 5-kg plots plants in the 0-Mg half-plots were less developed than in the +Mg ones. Plants in the AS plots failed completely. Samples from the various plots were analysed in succeeding years (Table 12).

TABLE 12

Mn-content of *Cichorium intybus* plants from experimental plots

Plot	Year	Mn ppm		
		0-Mg	+Mg	Diff. 0-Mg and +Mg
I_0	1952	1300	1132	+168
I_0	1953	1906	1638	+268
II_0	1955	504	577	− 73
III_0	1955	615	430	+185
I_5	1952	730	705	+ 25
I_5	1953	993	872	+121
I_5	1955	567	294	+273
II_5	1952	1275	644	+631
III_5	1955	615	430	+185
II_{10}	1953	509	356	+153
III_{10}	1953	338	249	+ 89
ASI	1953	605	419	+186
ASI	1955	682	1050	−368
ASII	1955	521	501	+ 20

In the first years, when the differences were very obvious, the 0-Mg plants in corresponding plots contained more Mn than the +Mg plants.

Experiments in nutrient solutions

The results are presented in Table 13.

TABLE 13

Mn-content of *Cichorium intybus* in modified nutrient solutions

Solution	Mn ppm			Symptoms
	Solution	Plants	Diff. with normal	
von der Crone				
$MgSO_4$ 0.4 g	20	1063	−571	Crinkle, sprightly
$MgSO_4$ 0.2 g	20	**1634**		id.
$MgSO_4$ 0 g	20	1268	−366	small, crinkle, necrotic margins
$MgSO_4$ 0.2 g	0.5			none
Solution II				
$MgSO_4$ 0.5 g	20	1302	+ 84	
$MgSO_4$ 0.25 g	20	**1218**		
$MgSO_4$ 0.12 g	20	1302	+ 84	

In Plate 2C the symptoms occurring in von der Crone solution are shown, the 0 $MgSO_4$—0.5 Mn differing only in size from the healthy plants grown in unmodified solution. Plate 3B shows that the injury occurring in an unlimed plot could be wholly reproduced in a nutrient solution with an excess of Mn and a deficiency of Mg.

When the experiment was repeated using distilled water, visible symptoms due to Mg-deficiency as such could be induced. Plate 2D shows the crinkled foliage with chlorotic mottling and down-turned tips. In the presence of Mn but in the absence of Mg plants were very pale and dwarfed.

The data of Table 13 do not point to a definite trend in the influence of Mg upon the uptake of Mn. The injury caused by excess of Mn and that by Mg-deficiency appear to have acted independently on the plants.

Thus the initial data gathered in the experimental field, which seemed to point to a depressing action could not be corroborated by solution cultures.

g. OATS

Field experiments

Oats (var. Adelaar) were grown on the experimental field in

1951, 1952, and 1953. In the acid 0-Mg plots symptoms of Mg-deficiency, described by Wallace [28] as bead-like groupings of green-colouring matter (Plate 21), occurred regularly, while in the highly limed plots Mn-deficiency (grey-speck disease) was observed. The highest amount of Mn in samples of plant material from the acid plots was 561, the lowest 206 ppm. In samples from the highly limed plots it varied from 50 to 57 ppm. 0-Mg plants did not exceed the +Mg plants in Mn-content.

Solution-culture experiments

Table 14 shows that a lowering of Mg-supply markedly enhanced the uptake of Mn, when the concentration of the latter was high. The only visible symptoms in the leaves were those caused by Mg-deficiency. Although the Mn-content was often much higher than in the field, no visible symptoms of excess of Mn could be observed.

TABLE 14

Mn-content in oat plants grown in modified solution cultures

Solution	Mn ppm			Symptoms
	Solution	Plants	Diff. with normal	
Solution II				
1952 $MgSO_4$ 0.5 g	40	677	−106	none
$MgSO_4$ 0.25 g	40	**783**		none
$MgSO_4$ 0.125 g	40	1015	+232	Mg-deficiency
$MgSO_4$ 0.06 g	40	1213	+429	Mg-deficiency
von der Crone				
1953 $MgSO_4$ 0.4 g	50	774	0	none
$MgSO_4$ 0.2 g	50	**774**		none
$MgSO_4$ 0.1 g	50	827	+ 53	Mg-deficiency
$MgSO_4$ 0.05 g	50	1028	+254	Mg-deficiency
$MgSO_4$ 0 g	50	1177	+403	Mg-deficiency
$MgSO_4$ 0.4 g	0.02			healthy
$MgSO_4$ 0.1 g	0.02			healthy

Cultures with a very low supply of Mn (20γ/l), even when highly supplied with $MgSO_4$ (0.4 g) did not show any signs of Mn-deficiency so in this case no depressing action of Mg could be observed.

Soil cultures

In 1952 experiments with soil in glass vessels were set up to investigate whether the application of Mg to limed soil would influence the incidence of grey-speck disease. Glass cylinders in duplicate were filled with 2 kg soil from a highly limed plot (pH 6.8) and supplied with 2 and 4 g $MgSO_4$ and one set was kept as control. At the close of the experiment the exchangeable Mn was estimated in the soil and hardly any differences were found (3.3 to 3.8 ppm) between the treatments. The available Mg estimated with the Aspergillus method [26] had increased with increasing supply. In the vessels with 4 g $MgSO_4$ the grey-speck symptoms initially appeared a few days later than in other treatments, but in the end plants in all vessels were equally affected. A repetition of this experiment gave identical results.

Hence neither by means of cultures nor in field experiments with a soil prone to induce Mn-deficiency was any depressing action of Mg on the uptake of Mn detected.

When the roots of the diseased plants, after having been thoroughly freed from adhering soil, were observed microscopically, they appeared perfectly sound and no trace of bacterial development round the root tips could be observed. Manganese deficiency was the direct cause of the grey-speck symptoms. This is in full agreement with the findings of Leach *et al.* [12].

h. WHEAT

Field experiments

Wheat (var. van Hoek's zomertarwe) was grown on the experimental plots in 1951, 1952 and 1953. No evidence of an action of Mg on the uptake of Mn was observed. In one AS plot only where in the 0-Mg part symptoms of Mg-deficiency in the leaves were noted, samples contained 527 ppm Mn, whilst from the +Mg part 369. Since these were the highest amounts obtained in any of the samples it seems that this cereal is very much lower in Mn-content as compared with other crops.

All the most highly limed plots bore crops with distinct signs of Mn-deficiency, described by Wallace [28] (Pl. 35) as intermittent, intervenal chlorotic streaks.

Solution-culture experiments

From Table 15 it is evident that Mg acted depressingly on the uptake of Mn.

No visible symptoms of Mn-toxicity or Mn-deficiency could be induced by changing the ratio of Mn and Mg in the nutrient solution.

TABLE 15

Mn-content of wheat grown on modified nutrient solutions

Solution	Mn ppm		
	Solution	Plants	Diff. with normal
Solution II			
$MgSO_4$ 0.25 g	50	**493**	
$MgSO_4$ 0.06 g	50	649	+156
$MgSO_4$ 0.25 g	20	**378**	
$MgSO_4$ 0.06 g	20	355	− 23
von der Crone			
$MgSO_4$ 0.2 g	50	**461**	
$MgSO_4$ 0.1 g	50	787	+326
$MgSO_4$ 0.05 g	50	718	+257
$MgSO_4$ 0 g	50	743	+282
$MgSO_4$ 0.4 g	0.02	no symptoms	
$MgSO_4$ 0.1 g	0.02	no symptoms	

i. RYE

Field experiments

Rye (var. Petkuser zomerrogge) was grown 1951 and 1952 in the experimental plots. Mg-deficiency symptoms occurred frequently in the 0-Mg half-plots. In 1951 only in (AS—0-Mg) half-plots plants showed other symptoms: leaf tips were rusty red, twisted and speckled with brown in the green parts of the leaves. The plants remained small. In 1952 similar symptoms were noted on the same plots. In that year samples were analysed for Mn and only the plants from the 0-Mg treatments of the AS plots containing 426 ppm surpassed those from the +Mg parts which contained 320 ppm. These amounts are very low when compared with those of other crops

In the highly limed plots no symptoms of Mn-deficiency could be detected. The Mn-content of the plants varied from 18 to 49 ppm.

Solution-culture experiments

The results are shown in Table 16.

TABLE 16

Mn-content of rye grown in modified Solution II

Solution	Mn ppm			
	Solution	Plants	Diff. with normal	
$MgSO_4$ 0.25 g	50	**677**		
$MgSO_4$ 0.12 g	50	1038	+361	
$MgSO_4$ 0.06 g	50	1028	+351	Specks
$MgSO_4$ 0.25 g	20	**474**		
$MgSO_4$ 0.12 g	20	470	− 4	
$MgSO_4$ 0.06 g	20	384	− 90	

Apparently in the presence of much Mn, Mg can depress its uptake by the plants. The absolute amount taken up, however, is very low.

j. BARLEY

In order to ascertain the symptoms of excess of Mn and of deficiency of Mg in barley, this crop (var. Kenia zomergerst) has been grown in nutrient solutions. When 20 or 30 ppm Mn was added to Solution II minute dark spots occurred on the distal part of the leaves and the leaf tips became necrotic. In mature plants the young leaves did not show any symptoms. (Cf Wallace [28] – Pl. 16, and the adequate description of Emerton Williams and Vlamis [3]). When grown without a supply of $MgSO_4$ plants were fairly small and of a pale-green colour. On the leaves extended necrotic spots occurred with a dark-coloured, often sharply edged border round a pale, dry central part. (Cf Wallace – Pl. 12).

Field experiments

From 1951 to 1953 barley was grown on the experimental plots. The symptoms of excess Mn were rarely observed, in fact only in the unlimed and AS plots in 1951. The symptoms were sometimes more conspicuous in the 0-Mg parts, sometimes no difference occurred. In the 0-Mg part of I_0, where the symptoms were more severe, the Mg-content was 865 ppm, but in the +Mg part 590 ppm. In 1952 Mg-deficiency was conspicuous in the 0-Mg parts

of the unlimed plots and in both halves of the AS plots. As far as the samples have been analysed for Mn the highest content was 476 ppm, *i.e.* markedly lower than in other crops.

In the plots limed with 30 and 60 kg symptoms of Mn-deficiency were frequent, consisting of small purplish brown or brown spots or stripes, which occurred intervenally in parallel rows, mostly in the distal part of the leaf. Tips were chlorotic.

Solution-culture experiments

The results are shown in Table 16a.

TABLE 16a

Mn-content of barley grown on modified nutrient solutions				
Solution	Mn ppm			Symptoms
	Solution	Plants	Diff. with normal	
Solution II				
1950 $MgSO_4$ 0.25 g	50	**666**		Mn-excess
$MgSO_4$ 0	50	889	+223	Mn-exc., Mg-defic.
1950 $MgSO_4$ 0.25 g	20	**452**		Mn-excess
$MgSO_4$ 0	20	866	+414	Mn-excess
1950 $MgSO_4$ 0.25 g	10	295		healthy
$MgSO_4$ 0	10			healthy
1951 $MgSO_4$ 0.25 g	50	**776**		Mn-excess
$MgSO_4$ 0.06 g	50	981	+205	Mn-excess
$MgSO_4$ 0	50	1369	+593	Mn-exc., Mg-defic.
Von der Crone				
1953 $MgSO_4$ 0.2 g	50	**613**		Mn-excess
$MgSO_4$ 0.1	50	840	+227	Mn-excess
$MgSO_4$ 0.05 g	50	904	+291	Mn-excess
$MgSO_4$ 0	50	921	+308	Mn-exc., Mg-defic.

The uptake of Mn, even when the content in the solution was as high as 50 ppm, remained moderate. In general symptoms of Mn-excess were less conspicuous in mature plants.

In solution cultures Mg depressed the uptake of Mn.

k. FLAX

Field experiments

Initially in the acid plots of the experimental field flax plants

(var. Concurrent) remained dwarfed with the leaf tips brown and shrivelled and the top parts sometimes of a very pale green (Plate 3C). In later years the injury was less severe, and finally occurred only on the 0-Mg halves of the acid plots or might even be absent. This raised the question, whether the injury might be ascribed to excess of Mn, or to Mg-deficiency or to both.

Table 17 gives data for succeeding years.

TABLE 17

Mn-content of flax in samples from corresponding half-plots						
Year	Plot	0-Mg		+Mg		Mn ppm, difference 0-Mg − +Mg
		Mn ppm	Development	Mn ppm	Development	
1953	I_0	1467	dwarfed	2057	normal	−590
1952	II_0	1709	dwarfed	1674	short	+ 35
1953	II_0	1524	short	1513	normal	+ 11
1954	II_0	510	short	533	normal	− 23
		504	normal			− 29
1955	II_0	755	sprightly	520	normal	+235
1956	II_0	663	normal	663	normal	0
1952	ASI	1339	dwarfed	2267	short	−928
1953	ASI	2728	dwarfed	2778	normal	− 50
1955	ASI	1507	short	1312	normal	+195
1956	ASI	655	normal	681	normal	− 26

The data of the last column do not point to a depressing action of Mg on the uptake of Mn. Sometimes the dwarfed plants appeared to be lower in Mn-content than the better developed ones. In those cases excess of Mn could hardly be the only cause of the injury.

In 1955 the Mg-content of the samples was also estimated.

TABLE 18.

Mg-content of flax in samples from corresponding half-plots						
Year	Plot	0-Mg		+Mg		Mg ppm, difference 0-Mg − +Mg
		Mg ppm	Symptoms	Mg ppm	Symptoms	
1955	II_0	892	leaf scorch	2150	none	−1258
		1022	none			−1128
1955	ASI	1928	leaf scorch	2572	none	− 644
1955	I_{15}	1000	leaf scorch	2640	none	−1640

Table 18 presents the results. All samples from +Mg half-plots surpass the corresponding 0-Mg samples in Mg-content. In plot I_{15} where the Mn-contents of plants in the two halves was similar the Mg-content of the 0-Mg part is much lower than in the sample from the +Mg part. Here the leaves showed symptoms which when compared with those induced in solution culture appeared characteristic of Mg-deficiency. Apparently in the experimental plots Mg-deficiency is the preponderant cause of the injury which occurs.

Millikan has tried to determine by means of symptoms in the leaves the cause of injury in flax plants. He describes [18] those induced by 25–100 ppm Mn in the nutrient solution: – "In some leaves the necrosis appeared not at the ultimate tip but close to it in the form of minute dark spots on the edges of the leaves. These necrotic spots soon enlarged until the whole of the lower half of the leaf remained practically normal green in colour". Very good photos of this syndrome are presented [20], which he describes as "lower leaf scorch". He notes, however, a stunting of the plants with chlorosis in the top, which is reminiscent of Fe-deficiency and dependent upon the amount of iron in the nutrient solution. Identical symptoms of lower leaf scorch have also been produced in highly acid soils by heavy applications of $MnSO_4$. He mentions later [19] that the "iron-deficiency chlorosis" of the plants occurred in spite of the fact that soil sterilization greatly increased their internal Fe-concentration. This indicates that in this instance it was not iron absorption but its utilization in the tisues of the plant which was adversely affected by an excessive absorption of manganese. Here the symptoms of "lower leaf scorch" as they were noted in the field are described as follows: – "The first signs of necrosis usually occur either at the ultimate tip or very close to it on one or both edges of the leaf". It is noteworthy that in these plants which were considered to be affected by excess of Mn, the highest content of Mn was 547 ppm and in some cases even low as 22. As the symptoms described above agree completely with symptoms which I could induce by Mg-deficiency, it seems to me that in in Millikan's concept the field symptoms must be ascribed to a lack of Mg.

Plate 3:

A. Flax in Nightingale solution, 0.5 mg Mn. *From left to right:* $^1/_{16}$ $Ca(NO_3)_2$—$^1/_{16}$ $MgSO_4$; $^1/_{16}$ $Ca(NO_3)_2$; $^1/_{16}$ $MgSO_4$; normal.

B. *Cichorium intybus. Left:* Von der Crone solution 0 $MgSO_4$—20 mg Mn. *Right:* Unlimed plot.

C. Flax from AS plot.

D. Flax in Solution II. *Left:* 0.5 mg Mn; *Right:* 50 mg Mn.

E. Flax in Solution II. *From lef to to right:* 0 $MgSO_4$—50 mg Mn; 0 $MgSO_4$—0.5 mg Mn; 0.25 g $MgSO_4$—50 mg Mn; 0.25 g $MgSO_4$—0.5 mg Mn.

te 3

Plate 4

Soil cultures

In 1954 experiments were run with soil in glass cylinders in duplicate. Samples of 2 kg from an AS plot not fertilized with Mg, where plants were severely injured, were used for the test. Soil properties were determined.

Soil	pH	available Mn ppm
At the start	4.5	19.9
After a month	4.15	17.2
15 $MgSO_4$ after a month		17.2

Apparently the additional Mg had hardly any effect on the availibility of Mn.

The culture vessels were each sown with 12 flax seeds. After 2 months the plants in the untreated soil showed leaf scorch and were smaller. Their Mn-content was 957 ppm. Those in the vessels where $MgSO_4$ had been supplied bore leaves that were healthy and had a Mn-content of 1235 ppm.

A repetition of this experiment, where larger amounts of $MgSO_4$ were supplied gave similar results.

In the soil from this very acid plot the poor development was apparently caused by Mg-deficiency.

Soil treatment	Plants	
	Description	Mn ppm
Untreated	Very low, old leaves necrotic	456
2 g $MgSO_4$	Plants higher, old leaves shrivelled	622
4 g $MgSO_4$	Highest plants, old leaves shrivelled	649

Solution-culture experiments

The symptoms of excess of Mn and Mg-deficiency were studied more in detail in nutrient solution. Data are taken up in Table 19.

Plate 4:

A. Flax in Nightingale solution, $^1/_{16}$ $Ca(NO_3)_2$—0.5 mg Mn.

B. Flax in Nightingale solution, $^1/_{16}$ $Ca(NO_3)_2$—0.5 mg Mn.

C. Flax in Solution II, 0-$MgSO_4$ 0.5 mg Mn. *Left:* Tapwater. *Right:* Dist. water.

D. Mangold from plot I_{15}. *Left:* No Mg added. *Right:* +Mg.

E. Mangold in Solution II, 1 mg Mn. *From left to right:* Normal; 0-$MgSO_4$; 0-$CaSO_4$; 0-$MgSO_4$, 0-$CaSO_4$.

TABLE 19

Mn-content of flax grown in modified Solution II				
Solution II	Mn ppm			Symptoms
	Solution	Plants	Difference with normal	
1952 $MgSO_4$ 0.25 g	20	**748**		none
$MgSO_4$ 0.12 g	20	598	— 150	none
$MgSO_4$ 0	20	790	+ 42	none
1954 $MgSO_4$ 0.5 g	30	1231	+ 330	leaf scorch
I $MgSO_4$ 0.25 g	30	**901**		leaf scorch
$MgSO_4$ 0.12 g	30	1406	+ 171	leaf scorch
1954 $MgSO_4$ 0.25 g	50			leaf scorch
II $MgSO_4$ 0.25 g	0.5			none
1954 $MgSO_4$ 0.25 g	50			leaf scorch
III $MgSO_4$ 0.12 g	50	3124		leaf scorch
$MgSO_4$ 0.06 g	50	1894		leaf scorch
$MgSO_4$ 0 g	50	3125		leaf scorch
$MgSO_4$ 0.25 g	0.5			none
$MgSO_4$ 0	0.5			Mg-deficiency
1954 $MgSO_4$ 0.5 g	50	3234	+ 336	none
IV $MgSO_4$ 0.25 g	50	**2898**		slight scorch
$MgSO_4$ 0	50	1748	—1486	Mg-defic., Mn-injury
1954 $MgSO_4$ 0.25 g	0.5			none
V $MgSO_4$ 0	0.5			slight Mg-defic.
$MgSO_4$ 0 dist. water	0.5			Mg-defic.

The data in column 4 of Table 19 do not point to any depressing action of Mg.

As 20 ppm Mn in the solution had not induced any leaf injury, more Mn was supplied in subsequent experiments. Thirty ppm (1954, I) induced leaf scorch, while 50 ppm (1954, II) affected the final development seriously (Plate 3D).

In 1952, whilst no leaf scorch was observed, a low supply of Mg reduced the development markedly. The effect of lack of Mg was demonstrated even more clearly in 1954, V where the development in nutrient solution with tapwater was compared with that in distilled water both in the absence of $MgSO_4$ (Plate 4C).

In 1954, III the effect of Mn-excess in the absence of $MgSO_4$ was investigated. Plants grown under such conditions reached a length of approximately 43 cm and were shorter than those grown

with Mn in excess (49 cm) or without Mg (60 cm), whilst plants in the normal solution reached a length of 70 cm (Plate 3E).

In 1954, III the early stages of leaf injury by Mg-deficiency were observed very clearly. The initial stage appears very suddenly and consists of a dark-coloured necrobiosis of the leaf tip or along the lower edge of the leaf where the tissue is limp, but not dry. Later this area grows necrotic and a yellow zone separates it from the green lower half of the leaf and at this stage the injury can no longer be distinguished from that caused by excess of Mn. In the latter the primary symptoms consist of a dark-coloured dry necrosis of the leaf tips or of dark specks scattered over the distal half of the leaves which later coalescence and are bordered by a yellow zone. The reader is referred to the description of Millikan (p. 362).

In 1955 the amount of Mg was estimated in the plants (Table 20).

TABLE 20

Mg-content of flax grown in modified Solution II

Solution		Mg ppm in plants	Symptoms
$MgSO_4$	Mn ppm		
0.25 g	20	1214	none
0.06 g	20	852	none
0	20	632	slight Mg-defic.
0.25 g	10	1268	none
0.06 g	10	786	slight Mg-defic.
0	10	572	Mg-defic.

Here again the amount of Mg estimated in the absence of $MgSO_4$ must have originated mainly from the tapwater supplied. The increase in intensity of the symptoms corresponds with a decrease in the Mg-content of the plants.

The results of the experiments with nutrient solutions corroborate the conclusion, based on the data from the experimental field, *viz* severe injury is caused by the simultaneous action of excess of Mn and deficiency of Mg.

The effect of Ca-deficiency

In Wallace [28] the injury caused by Ca-deficiency in flax is shortly described, whilst a characteristic picture of the final stage (Pl. 43) is presented.

The influence of Ca on the uptake of Mn was investigated by means of the Nightingale solution (Table 21).

TABLE 21

Mn-content in flax grown in modified Nightingale solution			
Solution	Mn ppm		
	Solution	Plants	Diff. with normal
1956 Normal	30	**1064**	
$^1/_8$ $Ca(NO_3)_2$	30	639	−425
1957 Normal	30	**1426**	
$^1/_{16}$ $Ca(NO_3)_2$	30	1249	−177
$^1/_{16}$ $MgSO_4$	30	1421	− 5
1958 Normal	30	**1480**	
$^1/_{16}$ $Ca(NO_3)_2$	30	880	−600
$^1/_{16}$ $MgSO_4$	30	1260	−220
$^1/_{16}$ $Ca(NO_3)_2$, $^1/_{16}$ $MgSO_4$	30	880	−600

Apparently, in contradistinction to other crops, the uptake of Mn by flax is always more depressed when the supply of Ca is decreased. The leaf scorch in all the plants is of a same nature. When the supply of both Ca and Mg is restricted, although the Mn-content is then at its lowest, plants are smallest.

The influence of the amount of Ca in the medium was further investigated in the presence of 0.5 Mn. When $^1/_{16}$ $Ca(NO_3)_2$ had been supplied very characteristic symptoms of Ca-deficiency could be observed. The top part of the stem bends downward and the stem collapses even while the top portion is still green. The point of attack of the injury is in a short zone on the stem some centimeters below the inflorescence which loses its turgor while still green and after a short interval decays. The distal portion of the stem then shrivels through lack of moisture. Sometimes this shrivelling of the top part will set in directly without collapsing of the stem zone. In Plate 3A the bending of the tops of the stems can be clearly recognized. When, however, $Ca(NO_3)_2$ and $MgSO_4$ were restricted simultaneously no such bending occurred, nor was it observed when Mn-excess and Ca-deficiency coincided.

As a result of the die-back of the top of the stem axillary buds develop into side-branches (Plate 2D). As they develop the axes of the latter will also collapse below the inflorescence or the pedicels,

although the flowers up to that moment have developed quite normally. The meristem of the flower bud does not suffer from lack of Ca (Plate 4B).

Besides this very characteristic symptom of Ca-deficiency in the flax plant, mature leaves may show symptoms of leaf scorch which cannot be distinguished from those caused by Mn-excess or Mg-deficiency. The cause of injury in flax plants can hardly be decided by studying the symptoms shown by mature leaves.

l. MANGOLD

Field experiments

The very poor development of mangolds (var. Groenkraag) in acid plots has already been described by the author [14]. The direct cause of the injury, however, was not established. Neither did Hewitt [8] succeed in reproducing the field symptoms.

In 1952, 1955, and 1957 mangolds were included in the field experiments in order to study a possible action of Mg. In those years their development was very irregular in the more acid plots, irrespective of the supply of Mg. In 1952 the development in the AS plots was a complete failure. As far as possible, however, comparable samples were gatherd with a view to establishing, whether Mg would depress the uptake of Mn. The Mn-content of the plants from the +Mg plots exceeded that of plants without Mg-supply in nine of the observed case, twice it was lower. Mg had apparently not exerted a depressing action on Mn-uptake. In the 0-Mg half-plots, however, leaves often showed a blackening which began at the margins and dark fungous spots occurred. The latter would have been due to saprophytic fungi in beets.

In healthy plants the Mn content varied between 310 and 830 ppm in poorly developed ones between 499 and 522, while in certain samples, the development of which had been noted as fairly good, it varied between 908 and 1236 ppm. In accordance with earlier observations, where the highest amount estimated in affected plants was 947, the field injury could not be ascribed to toxic action of Mn.

Solution-culture experiments

The influence of Mg on the uptake of Mn did not follow a definite

trend (Table 22). In 1957 20 ppm Mn induced a slight chlorosis.

TABLE 22

Mn-content of mangolds grown on modified Solution II

Solution II	Mn ppm			Weight g p.pl.	Symptoms
	Solution	Plants	Diff. with normal		
1954 $MgSO_4$ 0.25 g	20	**1722**		45 (6)	none
$MgSO_4$ 0	20	1743	+ 21	39.3 (6)	chlorosis
$MgSO_4$ 0 dist. water	20	2680	+958	10.1 (6)	chlorosis, spots
$MgSO_4$ 0.25 g	0.5			31.7 (6)	none
$MgSO_4$ 0	0.5			34 (6)	fungous spots
$MgSO_4$ 0 dist. water	0.5			12 (6)	chlorosis, spots
1957 $MgSO_4$ 0.25 g	20	**1374**		43.8 (6)	slight chlorosis
$MgSO_4$ 0.06 g	20	1257	−117	45 (4)	slight chlorosis
$MgSO_4$ 0.25	1			41 (2)	healthy

The total absence of Mg in the solution with distilled water causes, however, a characteristic injury. Plants were small with dark withered leaves, in mature leaves intervenal chlorosis and many fungous spots. These symptoms due to Mg-deficiency agree closely with the description given by Hale *et al.* [6] and Wallace (Pl. 121) and with the injury noted in the 0-Mg part of the I_{15} plot in the experimental field (Plate 4D).

The possibility that Ca-deficiency might be directly or indirectly injurious, already considered by Hewitt [7], has been investigated by means of Solution II where Ca was left out by omitting $CaSO_4$ and substituting Na_3PO_4 for $Ca_3(PO_4)_2$. As $MnSO_4$ is only partly soluble in such a solution, the effect of Ca-deficiency in the presence of sufficient Mn for normal development can alone be studied in this way.

Plants grown in the unmodified solution were healthy. When $MgSO_4$ was left out, plants showed marginal chlorosis and a blackening with fungous spots. Where Ca had been omitted plants were healthy and developed best. In the absence of Mg and Ca chlorosis and fungous spots were manifest (Plate 4E).

The influence of Ca-deficiency in the presence of Mn excess has been studied in Nightingale solution.

TABLE 23

Mn-content of mangolds grown in modified Nightingale solution					
Solution	Mn ppm			Weight g/pl.	Symptoms
	Solution	Plants	Diff. with normal		
Normal	20	**1063**		44.7 (3)	slight chlorosis
$^1/_{16}$ $MgSO_4$	20	1072	+ 9	35.6 (3)	slight chlorosis
$^1/_{16}$ $Ca(NO_3)_2$	20	1236	+173	44 (3)	slight chlorosis
Normal	1			41 (2)	healthy
$^1/_{16}$ $MgSO_4$	1			37.5 (2)	healthy
$^1/_{16}$ $Ca(NO_3)_2$	1			41.2	healthy
Normal	20	**1233**		25.3 (3)	slight marmoring
0 $Ca(NO_3)_2$	20	913	−320	29.2 (4)	marmoring
Normal	30	**1762**		29 (3)	slight marmoring
0 $Ca(NO_3)_2$	30	1215	−547	39.8 (4)	marmoring
Normal	1			22.5	healthy
0 $Ca(NO_3)_2$	1			38.2	healthy

Table 23 does not furnish an indication of a depressing action of Ca on the uptake of Mn. By substituting $NaNO_3$ for $Ca(NO_3)_2$ no injury ascribable to Ca-deficiency was ever noted. In fact the plants were generally better developed and quite healthy. These experiments, however, were not done with distilled water.

In the Nightingale solution Mn-excess also induced some slight chloritic mottling in the plants, which, however, had no effect on the final weight.

The attempts to reproduce the initial field symptoms, independent of Mg-deficiency met with no success.

m. LUPINUS LUTEUS AND *ORNITHOPUS SATIVUS*

Field experiments

Lupinus luteus and *Ornithopus sativus*, both known as acid-tolerant crops, were grown in 1950 and 1951 on the experimental plots. Both developed perfectly well on all the plots and no trace of injury was noted. They developed equally well on +Mg and 0-Mg half-plots. When the content of Mn in samples from the acid plots was estimated, these contained high amounts of Mn.

In lupin the highest amount was 2780 ppm in I_0 in *Ornithopus* 3020 ppm in ASI. Plants from the 0-Mg half-plots did not exceed those from the +Mg halves in Mn-content.

Both crops appear to be highly tolerant of large amounts of Mn.

4. GENERAL DISCUSSION

As has been reported in former papers by the author the difference in absorption of Mn by various crops is very marked. In many of the crop plants the green weight of the yield has been estimated, although few of the results are included in this paper. In some cases plants with severe symptoms of Mn-injury weighed no less than those which exhibited less obviously or lacked symptoms. For instance the approximate weight per plant of lucerne in Nightingale solution with $^1/_8$ $Ca(NO_3)_2$ and 10 ppm Mn was 1.33 g and with $^1/_{16}$ $Ca(NO_3)_2$ and 0.5 ppm Mn also 1.33 g while *Brassica napus* in von der Crone solution with 10 ppm Mn yielded 6.5 g, with 5 ppm Mn 4.65 g, and with 2.5 ppm Mn 4.77 g per plant.

Although generally injury due to Mn-excess inhibits plant development, the high content of Mn is not due to dwarfing, but conversely the dwarfing is the result of the high content.

When experiments are repeated, the difference in content of a single crop plant in similar nutrient solution may be significant. External conditions apparently influence the degree of absorption. Single *et al.* [25] reported the same phenomenon: – when working with wheat plants in great heat the amount of Mn ppm might be doubled. So the amounts are only comparable in individual experiments.

As has been observed already [14] great differences exist in the amount of Mn taken up by various crops from the same soil. All the cereals grown were low in uptake and in the case of rye this may well be one of the reasons of its tolerance for acidity in soils.

Lupine and *Ornithopus sativus* which did not show any injury even on the most acid plots, however, take up large amounts and their tolerance for soil acidity may in part be due to their tolerance for Mn.

When the amounts of Mn taken up by the various crops are compared with those found by other workers, they appear very high.

For the sake of comparison the content of healthy *Calluna vulgaris* collected in a wood nearby the experimental field on a similar sandy soil has been estimated. The foliage contained 1157 ppm, the twigs 819. In samples of wild-grown *Calluna vulgaris* collected in various parts of the Netherlands, the content of the foliage varied from 321 to 908 ppm, so the amount estimated in the Wageningen sample exceeded all the others. More unexpected still was the amount found in healthy *Vaccinium myrtillus* grown in the same wood near Wageningen: in the foliage it amounted to 12107 ppm, in the twigs to 2422 ppm! Apparently plants which are resistant to Mn-toxicity may take up exceedingly large amounts of this metal.

It is well known that Mn is an activator of many enzymes, among which are those which play a key role in general metabolism (Hewitt [9], Anderson and Evans [2], Mudd and Burris [21], Eyster *et al.* [4]). As Mn may enter upon so many phases of metabolism, a deleterious action of Mn-excess can be explained with difficulty. In 1954, however, Hewitt [10] using beets and spinach beets as experimental plants pointed to a special role which Mn-excess might play. In this paper he made the following statement:

"The existence of an acetone-soluble Mg-fraction other than chlorophyll was shown. Mn did not reduce the total Mg, but reduced the chlorophyll, increased the non-chlorophyll acetone-soluble Mg, but reduced the other fractions. This might indicate that this metal prevented the conversion of a precursor possibly allied to protochlorophyll or chlorophyll itself".

In this connection it is of interest that I noticed a slight chlorosis without other symptoms of injury in mangolds when grown in Nightingale solution with 20 or 30 Mn ppm.

As soon as the depressing influence of Mg on the uptake of Mn had been noted, it was deemed worthwhile to study it more in detail, as in fact Mg-deficiency may occur in acid soils along with Mn-excess.

Although there exists an extensive literature on the antagonistic action of heavy metals on the absorption of Mn, the influence of Mg has been very rarely mentioned.

Parberry [23] in a paper on scald of beans reports: "Mg-deficient plants contain considerably smaller amounts of Mg, lime and K than apparently healthy plants in the same plantings and have a considerably higher content of Mn, P and N. The Mn-content of the chlorotic, Mg-deficient plants is

inordinately high, reaching the extreme 1,800 ppm and is more than double that in the associated green plants, which also contain much Mn".

Hewitt [10] reports that Mn did not reduce the total Mg in beets.

Emerton Williams and Vlamis [3] have studied the effect of various cations on the uptake of Mn from Hoagland solution by barley. Ca had the strongest effect and reduced the content of the old leaves to 45%, while with K and Mg this reduction amounted to 25%. Considering the data reported by me [14], they point to the probability that Ca and Mg might have depressed the uptake of Mn.

As for micro-organisms Abelson and Aldous [1] state that Mn and Zn are not toxic to *Escherichia coli*, unless the concentration of the Mg is very low. Decreasing the Mg-level results in a greater uptake of Mn.

Gale [5] mentions that the tolerance of Mn of *Staphylococcus aureus* is augmented by Mg.

The experiments carried out with nutrient solutions were all set up in order to study the influence of Mg on the Mn-uptake. The reverse, *viz* the action of Mn on the uptake of Mg has not been studied, so true antagonism of Mg—Mn has not been established.

Comparing the results obtained experimentally with the various crop plants the depressive action of Mg on the uptake of Mn varies greatly. While this action is very considerable in *Phaseolus* and potatoes [15], so considerable that it gave the impulse for further study, it is less marked in *Brassica napus* and hardly exists in lucerne. In *Cichorium intybus* the field experiments suggested the existence of a depressive action, but this could not be corroborated by solution cultures. When cereals in the nutrient solution had been abundantly supplied with Mn, Mg suppressed its uptake.

In the highly limed plots Mn-deficiency in wheat and oats occurred in a same measure in +Mg and 0-Mg half-plots. For oats this was corroborated by soil cultures. One year in the highly limed plots symptoms of Mn-deficiency occurred in potatoes and they were also present simultaneously in the corresponding half-plots. Apparently Mg does affect the uptake of Mn, when the latter is available in low amount.

When $MgSO_4$ had been omitted from the nutrient solution, the Mg-content of the plants might still be considerable (*Phaseolus*, flax). When, however, the nutrient solution had been made up with distilled water instead of tapwater, symptoms of Mg-deficiency in the plants were much more manifest (*Cichorium intybus*, flax, mangold). Apparently the tapwater is the main casual source of Mg.

Characteristic injury due to Mg-deficiency as such could be

observed in *Phaseolus* and lucerne, where plants might show its symptoms in the older leaves, whilst in the younger leaves symptoms of Mn-excess might be manifest. Field symptoms in flax and *Cichorium intybus* could be reproduced by the additive action of Mg-deficiency and Mn-excess. In mangold which is not or hardly affected by Mn-excess, an injury noted in the field could be reproduced by Mg-deficiency. The cause of the dwarfing which occurred initially in the most acid plots could not be established.

Field observations cannot furnish information on the direct action of Ca on the uptake of Mn, as Ca by raising the pH may influence the availibility of Mn.

Hewitt [7] by working at identical levels of pH has furnished proof that Ca as such may depress the uptake of Mn considerably in various crop plants.

Taper and Leach [27] report a decrease in the absorption of Mn and Fe by dwarf kidney beans when the content of Ca in the solution culture is increased.

Emerton Williams and Vlamis [3] note a strong influence ot Ca on the uptake of Mn by barley.

Quellette and Dessureaux [14] growing lucerne in sand culture and estimating Ca and Mn in the yield, report that increase of the Ca-level in the nutrient solution counteracts to some extent the action of Mn and that the plants which grew best in toxic concentrations of Mn contained more Ca.

As far as the influence of Ca has been studied in this investigation, it exerted in *Phaseolus* a stronger depressing influence on the uptake of Mn than Mg, in *Brassica napus* this difference was still more manifest, in lucerne Ca acted strongly, while Mg did not, in mangold it did not influence the uptake, while in flax the intake of Mn decreased even when the Ca-level was lowered.

Thus Mg and Ca may influence the uptake of Mn strongly, but it must be kept in mind that crop plants vary widely in this respect.

5. SUMMARY

In acid soil injury caused by excess of manganese in *Phaseolus vulgaris* could be diminished by fertilising with magnesium. The plants supplied with $MgSO_4$ were markedly lower in Mn-content. In nutrient solution this depressing action of Mg on the uptake of Mn could be reproduced. Ca acted similarly on the uptake of Mn.

In field experiments with lucerne the action of Mg on the uptake of Mn was hardly noticeable. In nutrient solutions lowering the level of Mg did

not affect the uptake of Mn, lowering the level of Ca strongly decreased the uptake of Mn and the severity of the injury.

In solution cultures of *Brassica napus* lowering the level of Mg acted slightly, of Ca very strongly on the injury and the uptake of Mn.

In *Glycine hispida* Mg acted markedly on the uptake of Mn in field experiments.

For *Cichorium intybus* field experiments seemed to point to an influence of Mg on the uptake of Mn. In solution cultures an independent action of Mn-excess and Mg-deficiency could be shown to occur, both causing injury. Field symptoms could be reproduced by this additive action.

Cereals tested took up much less Mn than other crops. In field experiments Mg did not influence the uptake of Mn. Mg influenced the uptake of Mn in nutrient solutions when the concentration of the latter was very high. Increasing the supply of Mg did not favor the occurrence of grey speck in oats.

In the experimental field Mg did not act upon the uptake of Mn by flax. In solution cultures the initial leaf symptoms of Mg-deficiency could be distinguished from injury through excess of Mn. Changing the Mg-level did not influence the uptake of Mn. Severe field symptoms could be reproduced by the additive action of Mn-excess and Mg-deficiency. Lowering the Ca-level induced here a decrease in the uptake of Mn. Ca-deficiency induced a characteristic injury of the stem just below the inflorescence.

Initially mangolds were very dwarfed in acid soil although their Mn-content was moderate. Mg did not influence the uptake of Mn. In nutrient solutions no injury could be induced by excess of Mn and neither Mg nor Ca influenced the uptake of Mn. Part of the field symptoms could be reproduced by Mg-deficiency, but attempts to reproduce the severe field symptoms did not meet with success.

Lupinus luteus and *Ornithopus sativus*, both acid-tolerant crops, did not show any field injury by excess of Mn, although the content of the plants was very high. Mg did not influence the uptake of Mn.

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AUFNAHME UND VERTEILUNG DER KATIONEN Ca, Mg, K UND Na IN DER PFLANZE BEI VARIIERTER K- UND Mg-DÜNGUNG SOWIE BEI EXTRARADIKALER K-VERSORGUNG

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1. FRAGESTELLUNG

In einer früheren Arbeit [26] stellten wir bei Sonnenblumen fest, daß eine steigende K-Düngung in erster Linie den Mg- und Ca-Gehalt des Blattes negativ beeinflußt, während in den Stengeln der Ca- und Mg-Gehalt trotz erhöhter K-Düngung ansteigen kann. Die Ergebnisse deuteten darauf hin, daß ein hoher K-Gehalt des Blattes den Eintritt der Ca- und Mg-Ionen in das Blattgewebe behindert, und daß sich die Ionenkonkurrenz zwischen den genannten Elementen hauptsächlich im Blatt und weniger im Stengel abspielt.

Um zu sehen, ob diese Ergebnisse eine gewisse allgemeine Gültigkeit haben, wurden im Sommer 1958 Wasserkulturversuche mit 6 verschiedenen Dikotyledonen durchgeführt, die auf nachstehende Fragen ausgerichtet waren:

a) In welchem Pflanzenorgan (Blatt, Stengel und Wurzel) wirkt sich die Ionenkonkurrenz des K gegenüber Ca, Mg und Na am stärksten aus?

b) Wird der Gehalt der Pflanze an Mg, Ca und Na beeinflußt, wenn man ihren K-Gehalt durch eine extraradikale K-Gabe erhöht?

c) Wie wirkt eine steigende Mg-Düngung auf die Ca-, K- und Na-Gehalte in den einzelnen Pflanzenorganen?

2. VERSUCHSDURCHFÜHRUNG

Der Versuchsplan wird durch nachstehendes Schema charakterisiert:

K_1Mg_1	K_BMg_1	K_2Mg_2
K_1Mg_2	K_BMg_2	K_2Mg_2

K_1 bzw. Mg_1 bedeutet die niedrigste K- bzw. Mg-Gabe, K_B besagt, daß neben einer K-Gabe zur Nährlösung in Höhe von K_1 noch zusätzlich K über das Blatt gegeben wurde (= extraradikale K-Gabe), K_2 bzw. Mg_2 stellt die höhere radikale K- bzw. Mg-Gabe dar. Die Reihen K_B und K_2 lassen sich in ihren Kationengehalten mit den Reihen K_1Mg_1 bzw. K_1Mg_2, die Reihen Mg_2 mit den entsprechenden von Mg_1 vergleichen, so daß der Versuchsplan den Anforderungen der Versuchsfragen gerecht wird. Jede Reihe wurde in 6-facher Wiederholung mit 5 Liter fassenden Kunststoffgefäßen angesetzt. Abgesehen vom Mg wurden je Gefäß etwa die gleichen Nährstoffmengen gegeben wie in dem oben erwähnten Versuch mit Sonnenblumen [6];. Die Mg-Gabe wurde dagegen infolge der anderen Fragestellung wesentlich erhöht, um durch Mg-Mangel evtl. hervorgerufene Wachstumsdepressionen, Chlorosen und Nekrosen, die die zu beobachtende Ionenkonkurrenz beeinflussen können, nach Möglichkeit zu vermeiden.

Als Versuchspflanzen dienten Tomaten (*Solanum lycopersicum*), Tabak (*Nicotiana tabacum*), Ackerbohnen (*Vicia faba minor*), Gurken (*Cucumis sativus*), Sonnenblumen (*Helianthus annuus*) und Erbsen (*Pisum sativum*).

Für die Versuche wurden zwei verschiedene Nährlösungen verwendet, da die für Tabak, Vicia und Tomaten mit NH_4NO_3 als N-Quelle angesetzte Lösung bei Gurken nur ein kümmerliches Wachstum, verbunden mit Blatt- und Wurzelschäden zeigte. Der negative Einfluß einer NH_4-Düngung in stehender Wasserkultur wurde bei verschiedenen Pflanzen schon von Pirschle [21] beschrieben, so daß wir für Gurken, Sonnenblumen und Erbsen eine Nährlösung mit ausschliesslich Nitrat-N zusammenstellten.

Nährlösung für Tomaten, Tabak und Vicia faba (Gabe je Gefäß):

N (als NH_4NO_3) 1,00 g (Tomaten), 0,75 g (Tabak, *V. faba*)
P (als $Ca(H_2PO_4)_2$) 0,40 g
K als KCl und K_2SO_4 (1 : 1 mol.): K_1 = 1,20 g K (Tom., Tab.), 1,00 g (*V. faba*)
K_B = 1,20 g K (Tom., Tab.), 1,00 g (*V. faba*)
K_2 = 3,00 g K (Tom., Tab.), 2,50 g (*V. faba*)
Mg als $MgSO_4$: Mg_1 = 100 mg Mg
Mg_2 = 200 mg Mg

Na (als Na_2SO_4)	70 mg	Zn (als $ZnSO_4$)	1 mg
Fe (als Fe–Chelat)	20 mg	B (als H_3BO_3)	1,5 mg
Mn (als $MnSO_4$)	10 mg	Mo (als Na_2MoO_4)	0,1 mg
Cu (als $CuSO_4$)	1 mg		

Nährlösung für Sonnenblumen, Buschbohnen und Erbsen (Gabe je Gefäß)

N (als $Ca(NO_3)_2$) 0,75 g
P (als NaH_2PO_4) 0,30 g
K als KCl und K_2SO_4 (1 : 1 mol.): K_1 = 1,00 g K
K_B = 1,00 g K
K_2 = 2,5 g K

Mg als $MgSO_4$:	Mg_1 = 100 mg Mg		
	Mg_2 = 200 mg Mg		
Fe (als Fe–Chelat)	20 mg	Zn (als $ZnSO_4$)	1 mg
Mn (als $MnSO_4$)	20 mg	B (als H_3BO_3)	1,5 mg
Cu (als $CuSO_4$)	1 mg	Mo (als Na_2MoO_4)	0,1 mg

Beide Lösungen wurden sowohl beim Ansetzen wie auch nach jedem Wechsel der Lösung in der für jede Pflanze oben angegebenen Konzentration verabreicht.

Die Nährlösung mit NH_4NO_3 hatte einen pH-Wert um 5,1 mit einer die H-Ionenkonzentration erhöhenden Tendenz im Laufe der Vegetation, die Nitrat-Nährlösung hatte einen pH-Wert von 6,1, der sich im Verlauf der Vegetation infolge einer vergleichsweise gegenüber Ca stärkeren NO_3-Aufnahme noch etwas erhöhte. Beide Nährlösungen bewirkten bei den entsprechenden Pflanzen ein normales, ungestörtes Wachstum. Da die Kationengehalte zwischen den einzelnen Pflanzen nicht verglichen werden, ist die Unterschiedlichkeit der Nährlösungen für die Versuchsfrage ohne Bedeutung.

Die K-Menge, die pro Versuchsreihe (K_B) in Form einer 2% K-Lösung (KCl und K_2SO_4, 1 : 1 mol) auf die Blätter gesprüht wurde, kann verständlicherweise nicht quantitativ angegeben werden. Wir haben in den verschiedenen Wachstumsstadien der Pflanzen den Verbrauch an Blattdüngungslösung gemessen und dabei gefunden, daß je nach Alter und Pflanzenart das versprühte Lösungsvolumen bei einer Behandlung in einer Größenordnung zwischen 3 und 15 ml (= 60–300 mg K) je Versuchsreihe lag. Von dieser vergleichsweise hohen K-Menge dürfte jedoch nur ein geringer Prozentsatz von der Pflanze aufgenommen worden sein, zumal schon beim Besprühen dadurch Verluste auftreten, daß ein Teil der gesprühten Lösung neben das Blatt fällt. Für die Versuchsfrage ist es jedoch weniger bedeutsam, welche Menge K während der Versuchsperiode auf das Blatt gebracht wurde, als daß die extraradikale K-Gabe den K-Gehalt des Blattes tatsächlich erhöhte.

Es wurde eine Woche nach dem Ansetzen der Pflanzen mit der Blattdüngung begonnen, und sie wurde während der gesamten Versuchsdauer an jedem zweiten Abend durchgeführt. Sechs Tage vor der Ernte stellten wir die extraradikale K-Gabe ein, und einen Tag vor der Ernte wurden die Pflanzen aller Reihen mit aqua dest. abgesprüht, um evtl. oberflächlich anhaftendes K abzuwaschen. Wir haben hierbei alle 6 Versuchsreihen mit aqua dest. abgebraust, um gleichmässige Bedingungen einzuhalten. Die Kulturgefäße wurden vor der Blattdüngung jedes Mal mit Schaumgummimatten dicht abgedeckt, so daß in jedem Fall ein Eintropfen der Blattdüngungslösung in die Gefäße vermieden wurde. Bei *Vicia faba* und Sonnenblumen wurde vor jedem Lösungswechsel und vor der Ernte der K-Gehalt und das Volumen der Nährlösung bestimmt, so daß es uns möglich war, die gesamte der Nährlösung entzogene K-Menge zu berechnen und sie dem Gesamt-K-Gehalt der Pflanze gegenüberzustellen. Diese Maßnahme sollte vor allen Dingen in den Blattdüngungsreihen den Beweis liefern, daß K tat-

sächlich über das Blatt aufgenommen worden war, darüberhinaus sollte hiermit eine halbwegs quantitative Aussage über den Anteil des vom Blatt sorbierten Kaliums erreicht werden.

Bei Versuchsbeginn waren die Pflänzchen 5–10 cm hoch. Der Wachstumsverlauf war für alle Pflanzen normal und ungestört. Ein sehr schwacher Mg-Mangel wurde nur bei *Vicia faba* gegen Ende der Wachstumszeit (2.7.) in der Reihe K_BMg_1 und besonders in der Reihe K_2Mg_1 als Aufhellung zwischen den Blattadern der ältesten Blätter beobachtet.

Bei der Ernte haben wir die Pflanzen sofort in Blätter, Stengel und Wurzeln getrennt, wobei die Blattstiele mit zu den Stengeln genommen wurden. Die Wurzeln wurden mit *aqua dest.* gründlich gewaschen, um oberflächlich anhaftende Ionen zu entfernen. Die Wurzeln der Tomaten wurden versehentlich nicht geerntet, so daß hier entsprechende Analysenangaben fehlen. Die wesentlichen Daten der Wachstumszeit sind in Tabelle 1 zusammengestellt.

TABELLE 1

Die wesentlichen Daten der Wachstumszeit			
Pflanze	Beginn der Kultur	Ende der Kultur	Wechsel der Lösung
Tomaten	16.5.	18.6.	4.6.
Tabak	20.5.	22.7.	2.6. und 2.7.
Vicia faba	20.5.	8.7.	18.6.
Gurken	8.7.	6.8.	29.7.
Sonnenblumen	9.7.	15.8.	—
Erbsen	16.7.	23.8.	4.8. und 15.8.

Die Kationen Ca, Mg, K und Na wurden mit zweifacher Wiederholung flammenspektrometrisch bestimmt [24 25]. Analysen mit einer grösseren arithmetischen Streuung als $\pm$ 3,0% wurden noch einmal wiederholt, so daß die angegebenen Analysenwerte innerhalb der genannten Fehlergrenze liegen. Da die Mg-Bestimmung geringfügig von der früher angegebenen Arbeitsvorschrift abweicht [24], sei sie kurz erläutert.

Nach der trockenen Veraschung im Porzellantiegel wird mit 2 ml 2,5 n HCl aufgenommen, verrührt, 20 ml Äthylalkohol und 0,2 ml H_2SO_4 (1 : 2) zugegeben. Die ausgefallenen K- und Ca-Sulfate werden durch ein Faltenfilter abfiltriert und 10 ml des Filtrats auf die Ionenaustauschsäule gebracht. Es wird mit 2,5 n HCl eluiert. Zum Eluat wird keine HNO_3 gegeben.

3. ERGEBNISSE

a) *Die lufttrockenen Gewichte der einzelnen Pflanzenorgane*

Im Rahmen der gestellten Versuchsfragen interessieren die Gewichte der einzelnen Pflanzenorgane nur insoweit, als extreme Abweichungen durch Verdünnungs- oder Konzentrationseffekte die konkurrierende Wirkung der Ionen überdecken oder verzerren

TABELLE 2

Die Erträge an lufttr. Substanz der einzelnen Pflanzen und Pflanzenorgane in g/Gefäß

	Blatt	Stengel	Wurzel
Tomaten			
Mg_1K_1	4,4	6,0	
K_B	4,4	5,3	
K_2	5,0	6,9	
Mg_2K_1	4,7	5,5	
K_B	4,9	6,2	
K_2	3,4	5,0	
Tabak			
Mg_1K_1	2,78	2,10	2,71
K_B	3,01	1,70	2,03
K_2	2,59	1,59	1,37
Mg_2K_1	3,44	3,17	3,92
K_B	2,90	1,42	2,10
K_2	3,00	1,34	1,34
Vicia			
Mg_1K_1	9.7	15,0	3,9
K_B	9,8	12,7	3,6
K_2	10,4	14,3	3,5
Mg_2K_1	8,8	12,9	3,4
K_B	9,7	13,5	3,6
K_2	9,0	13,2	3,1
Gurken			
Mg_1K_1	5,1	2,24	1,43
K_B	4,9	2,22	1,09
K_2	2,6	1,10	0,48
Mg_2K_1	4,4	2,04	1,24
K_B	4,4	2,15	1,31
K_2	2,9	1,12	0,65
Sonnenblumen			
Mg_1K_1	8,0	17,8	3,68
K_B	7,4	17,3	3,47
K_2	7,8	16,8	4,20
Mg_2K_1	7,9	18,7	3,67
K_B	8,0	18,9	4,50
K_2	8,5	16,7	4,20
Erbsen			
Mg_1K_1	2,65	4,6	0,72
K_B	1,73	4,0	0,62
K_2	1,82	3,7	0,62
Mg_2K_1	2,10	4,3	0,91
K_B	1,67	3,4	0,57
K_2	1.78	3,6	0,57

können. Da durch eine erhöhte K- bzw. Mg-Gabe infolge Ionenkonkurrenz ein niedrigerer Gehalt anderer Kationen erwartet werden muß, kann eine Überdeckung nur dann eintreten, wenn durch die gesteigerte K- bzw. Mg-Gabe ein erheblicher Ertragsanstieg und damit an sich schon eine Verdünnung der Ionenkonzentration bzw. ein niedrigerer Gehalt anderer Kationen bewirkt wird. Die Tabelle 2 zeigt, daß dies weder für K noch für Mg der Fall ist. Im Gegenteil, bei Erbsen und besonders bei Gurken wurde der Ertrag durch die erhöhte K-Gabe beachtlich erniedrigt, so daß man bereits mit einem geringen Anstieg der Kationengehalte rechnen kann. Wenn trotzdem die Ionenkonkurrenz in den Gehaltszahlen der einzelnen Kationen deutlich zum Ausdruck kommt, so spricht das ganz besonders für die Stärke der konkurrierenden Wirkung.

Es darf also gesagt werden, daß die ermittelten Gehaltszahlen der einzelnen Kationen nicht durch Verdünnungseffekte hervorgerufen wurden. Es ist erwähnenswert, daß die höhere, ausschliesslich über die Wurzel zugeführte K-Gabe (K_2) eine sehr beachtliche Wachstumsdepression der Blätter, Stengel und Wurzeln bei Gurken bewirkte, die zusätzliche Blattdüngung dagegen zeigte diese depressive Wirkung nicht, obgleich die K-Gehalte in den Blattdüngungspflanzen etwa ebenso hoch sind wie in den Pflanzen mit höherer K-Gabe. Der Befund deutet darauf, daß die Konzentration und besonders die Ionenverhältnisse in der Nährlösung das Wachstum wesentlich beeinflussen können. Die Feststellung bei Gurken ist nicht zufällig; wir beobachteten in einem vorhergehenden Wasserkulturversuch mit Gurken ebenfalls eine beachtliche Ertragsdepression durch eine gesteigerte K-Düngung.

b) *Der Einfluss der K-Düngungsform auf den K-Gehalt der einzelnen Pflanzenorgane*

In Fig. 1 sind die K-Gehalte der einzelnen Pflanzenorgane der genannten 6 Dikotyledonen dargestellt. Es ist ersichtlich:

1. Die höhere radikale wie auch die zusätzliche extraradikale K-Gabe haben den K-Gehalt der Blätter, Stengel und Wurzeln (hier bis auf die Ausnahme bei Erbsen, K_B) erhöht.

2. Im Vergleich zur Blattdüngung hat die gesteigerte radikale K-Gabe (K_2) in den meisten Fällen einen höheren K-Gehalt der Wurzeln und Stengel hervorgerufen.

3. Die K-Gehalte des Blattes wurden bis auf wenige Ausnahmen

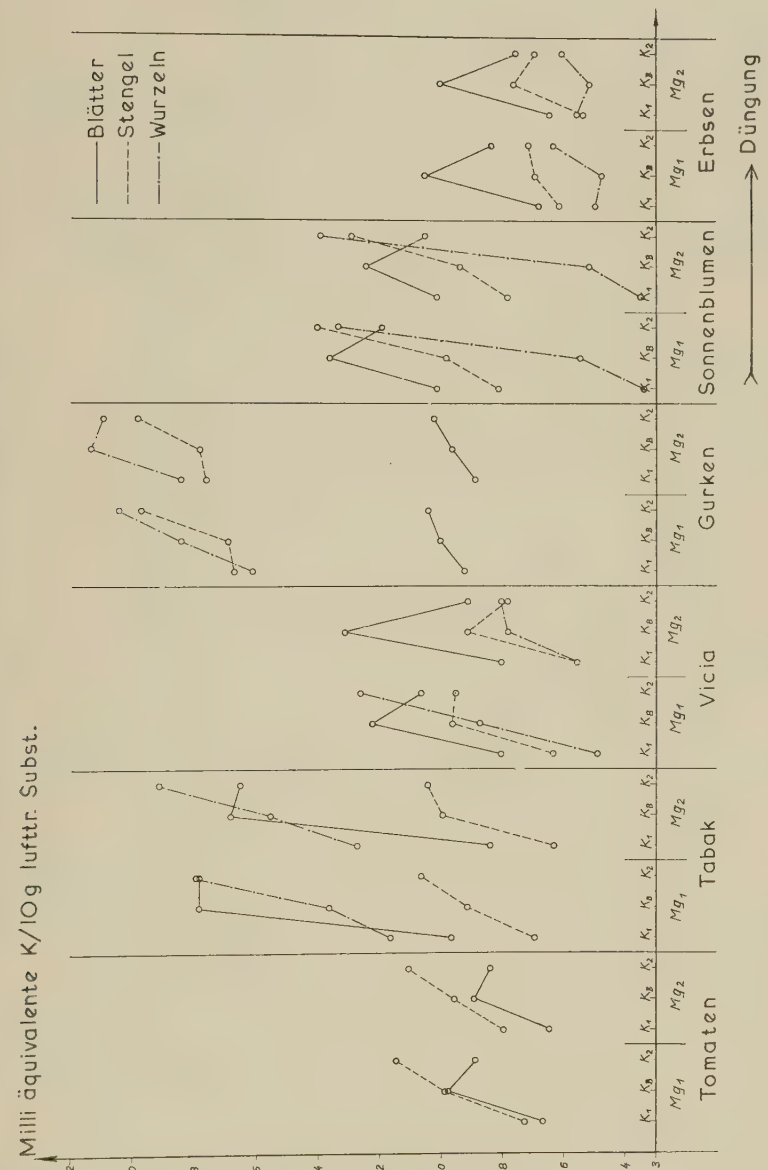

Fig. 1. Der Einflusz der K-Düngung auf den K-Gehalt der Blätter, Stengel und Wurzeln.

durch die extraradikale K-Gabe stärker erhöht als durch die gesteigerte radikale K-Düngung.

Bei einem Vergleich zwischen den Reihen K_2 und K_B darf also der lokalen Anwendung entsprechend gesagt werden, daß die Blattdüngung sich mehr auf den K-Gehalt des Blattes, die „Wurzeldüngung" sich mehr auf den K-Gehalt der Wurzeln und Stengel ausgewirkt hat. Die Erhöhung der K-Gehalte in Wurzel und Stengel bei Blattdüngung spricht für eine gute basipetale Beweglichkeit des K und bestätigt die Ergebnisse Bukovac's und Wittwer's [7].

c) *Der Einfluß der höheren radikalen K-Gabe auf den Mg-, Ca- und Na-Gehalt in den einzelnen Pflanzenorganen*

In Fig. 2 ist der relative Gehalt an Mg, Ca und Na der Reihen K_2 in Beziehung zum Gehalt der entsprechenden Standardreihe ($= K_1$) dargestellt, deren jeweiliger Mg-, Ca- und Na-Gehalt = 100 gesetzt wurde. Punkte, die also unter der „Linie 100" liegen, bedeuten einen niedrigeren Gehalt des betreffenden Kations im Vergleich zur Standardreihe. Der Figur 2 kann man entnehmen:

1. Im Blatt sind bei erhöhter radikaler K-Gabe bis auf eine Ausnahme (Na in Reihe Mg_1 bei Sonnenblumen) die Mg-, Ca- und Na-Gehalte erniedrigt worden.

2. Im Stengel ist die Beziehung nicht mehr ganz so eindeutig, jedoch ist auch hier die Tendenz der K_2-Düngung, den Gehalt der übrigen Kationen zu erniedrigen, größer als ihn zu erhöhen bzw. wirkungslos zu bleiben.

3. In der Wurzel sind die Abweichungen vom Standardwert sowohl nach oben als auch nach unten sehr groß. Die Tendenz, daß eine steigende K-Düngung den Gehalt der genannten drei übrigen Kationen negativ beeinflußt, ist auch hier vorhanden.

4. Eine grundsätzlich unterschiedliche Reaktion zwischen den Ionen Mg, Ca oder Na auf die erhöhte K-Gabe liegt nicht vor. Lediglich für die Wurzeln darf gesagt werden, daß sich hier die höhere K-Düngung bei allen Pflanzen besonders stark auf den Na-Gehalt ausgewirkt hat.

Zusammenfassend sei gesagt: Der negative Einfluß einer erhöhten K-Düngung zeigt sich für Ca und Mg am sichersten im Blatt. Stengel und Wurzel zeigen die gleiche Tendenz nicht mehr so ausgeprägt. Für Na hat sich die höhere K-Düngung am stärksten und sichersten in den Wurzeln ausgewirkt.

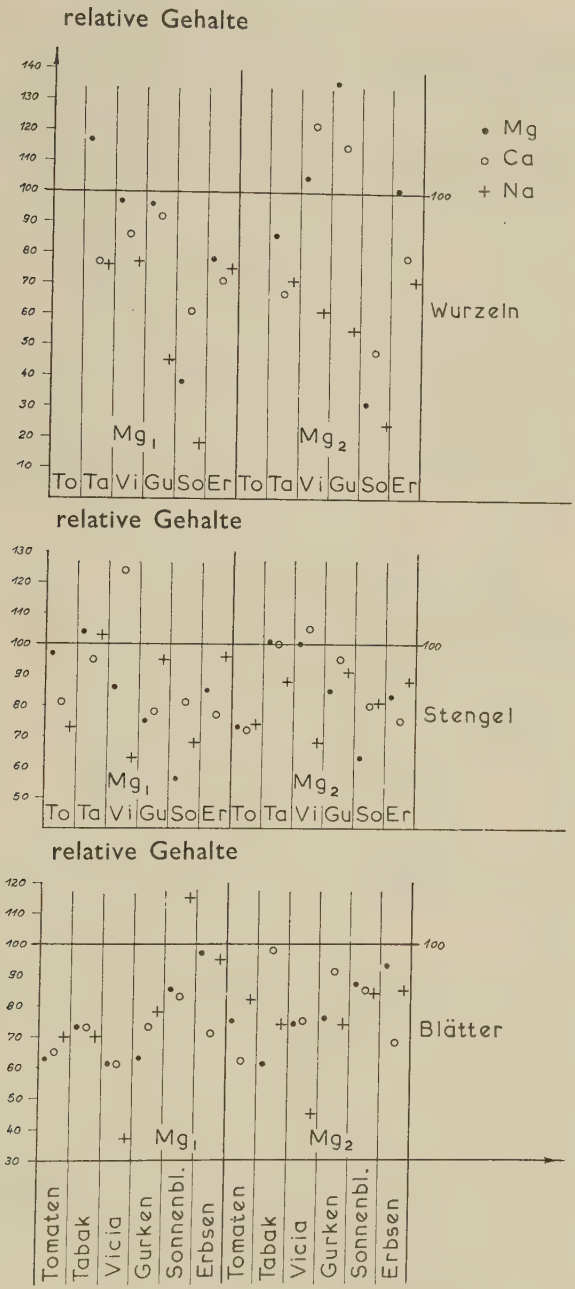

Fig. 2. Der Einfluss einer höheren radikalen K-Gabe (K_2) auf den Gehalt an Mg, Ca, und Na ($K_1 = 100$).

d) *Der Einfluß der zusätzlichen extraradikalen K-Gabe auf den Mg-, Ca- und Na-Gehalt in den einzelnen Pflanzenorganen*

Die Figur 3 entspricht in ihrer Darstellungsweise der Figur 2. Sie gibt die relativen Mg-, Ca- und Na-Gehalte der Reihen K_B im Vergleich zu den Reihen K_1 an. Es ist augenscheinlich, daß durch die

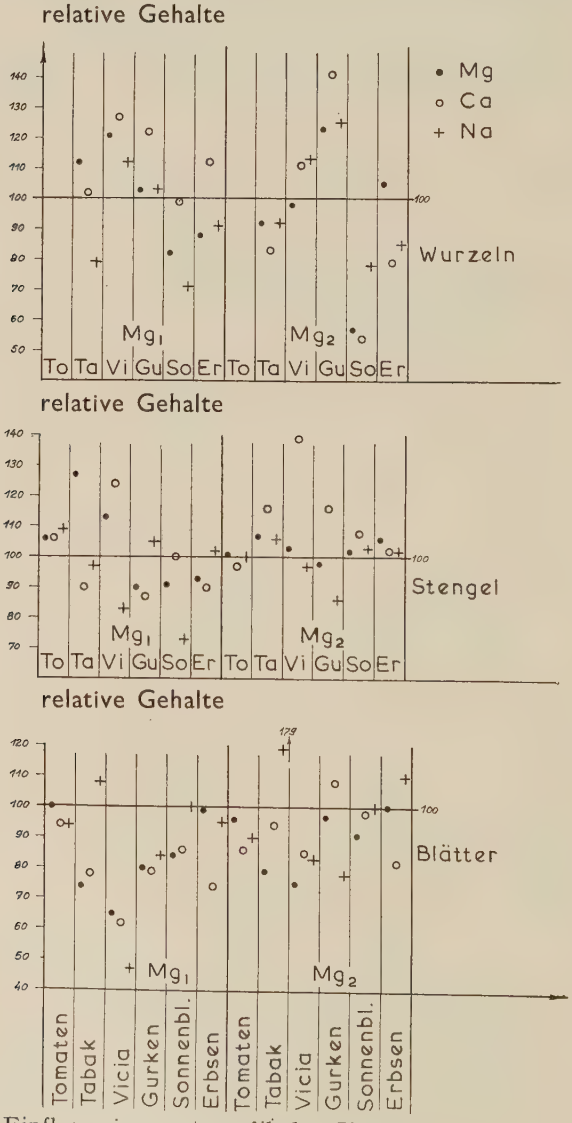

Fig. 3. Der Einfluss einer extraradikalen K-Gabe auf den Gehalt an Mg, Ca, und Na (ohne extraradikale K-Gabe = 100).

extraradikale K-Gabe lediglich im Blatt die Mg-, Ca- und Na-Gehalte erniedrigt wurden, während bei den Gehalten im Stengel und in der Wurzel kein gesicherter Einfluß der extraradikalen K-Gabe vorliegt. Der Befund deckt sich mit der Wirkung der K_B-Düngung auf den K-Gehalt. Hier wurde festgestellt, daß sie am besten im K-Gehalt der Blätter und weniger im K-Gehalt der Stengel und Wurzeln zum Ausdruck kommt (Fig. 1). Wie erwähnt, hat die extraradikale K-Gabe im Vergleich zu K_2 in den meisten Fällen einen höheren K-Gehalt im Blatt bewirkt. Trotzdem hat sie offenbar den Gehalt an anderen Kationen im Blatt nicht so stark erniedrigt wie die höhere K-Düngung über die Wurzel (siehe Figur 2 u. 3). Um die Höhe der absoluten Gehalte an Mg, Ca und Na wiederzugeben, sind in Tabelle 3 die Gehalte der gleich 100 gesetzten Bezugswerte von Figur 2 und 3 aufgeführt (d.h. der Düngungsreihen K_1Mg_1 u. K_1Mg_2).

TABELLE 3

Mg-, Ca- und Na-Gehalte der Düngungsreihen K_1Mg_1 und K_1Mg_2 (in Fig. 2 u. 3 = 100 gesetzt) in Milliaequivalenten/10 g lufttr. Subst.

Reihe	Blätter			Stengel			Wurzeln		
	Mg	Ca	Na	Mg	Ca	Na	Mg	Ca	Na
Tomaten									
K_1Mg_1	2,84	3,49	0,53	1,50	1,60	0,55	Tomatenwurzeln		
K_1Mg_2	4,32	3,49	0,50	2,10	1,45	0,57	wurden nicht		
							geerntet		
Tabak									
K_1Mg_1	3,06	8,63	1,41	0,69	2,02	1,52	2,67	7,93	1,12
K_1Mg_2	5,74	7,68	0,85	0,91	1,55	1,39	3,63	7,34	0,97
Vicia faba									
K_1Mg_1	2,44	3,04	0,76	1,00	1,05	0,65	1,08	1,10	2,61
K_1Mg_2	2,56	1,95	0,58	1,18	0,90	0,59	1,30	0,91	2,94
Gurken									
K_1Mg_1	3,92	24,2	0,63	2,17	10,8	2,11	1,18	3,89	2,08
K_1Mg_2	5,54	18,9	0,59	2,49	8,18	2,35	1,55	3,54	1,69
Sonnenblumen									
K_1Mg_1	2,20	8,08	0,26	1,74	4,29	0,41	2,42	4,34	12,3
K_1Mg_2	2,78	7,49	0,26	2,19	3,79	0,37	3,30	5,64	10,6
Erbsen									
K_1Mg_1	1,33	6,09	0,20	0,60	3,39	0,52	2,48	4,99	0,55
K_1Mg_2	1,78	5,69	0,20	0,78	2,94	0,58	2,53	4,99	0,52

e) *Die K-Aufnahme über das Blatt im Vergleich zur Aufnahme über die Wurzel bei Vicia und Sonnenblumen*

In den Tabellen 4 und 5 ist die gesamte durch die Pflanzenanalyse gefundene K-Menge der Pflanzen einer Versuchsreihe dem K-Entzug, der sich aus den K-Analysen der Nährlösung errechnete, gegenübergestellt. In den Reihen ohne extraradikale K-Gabe zeigen

TABELLE 4

Die K-Bilanz bei Sonnenblumen (g K/Versuchsreihe)						
Reihe	K_1Mg_1	K_1Mg_2	K_BMg_1	K_BMg_2	K_2Mg_1	K_2Mg_2
K-Menge in der Nährlösung bei Versuchsbeginn . . .	6,00	6,00	6,00	6,00	15,00	15,00
K-Menge in der Nährlösung bei der Ernte	0,20	0,35	0,35	0,50	5,60	5,90
der Nährlösung entzogene K-Menge	5,80	5,65	5,65	5,50	9,40	9,10
K-Menge in der Pflanze nach der Pflanzenanalyse *	5,63	5,54	6,80	7,10	9,10	8,60
% des aus der Nährlösung stammenden K. 100% = Gesamt-K-Menge in der Pflanze	103	102	83	78	102	109

* Die Menge wurde aus den K-Gehalten der Blätter, Stengel und Wurzeln errechnet.

TABELLE 5

Die K-Bilanz bei *Vicia faba* (g K/Versuchsreihe)						
Reihe	K_1Mg_1	K_1Mg_2	K_BMg_1	K_BMg_2	K_2Mg_1	K_2Mg_2
Gesamte in die Lösung gegebene K-Menge	12,0	12,0	12,0	12,0	30,0	30,0
K-Menge vor dem Wechsel + K-Menge vor der Ernte in der Nährlösung	7,0	7,5	6,8	7,3	22,2	25,0
Der Lösung entzogene K-Menge	5,0	4,5	5,2	4,7	7,8	5,0
K-Menge in der Pflanze nach der Pflanzenanalyse *	4,9	4,2	6,7	7,1	7,2	5,3
% des aus der Nährlösung stammenden K (100% = Gesamt-K-Menge der Pflanze)	102	107	78	66	108	94

* Die Menge wurde aus den K-Gehalten der Blätter, Stengel, Wurzeln und Früchte errechnet.

die zu vergleichenden Werte, der Entzug aus der Nährlösung und die K-Menge in den Pflanzen einer Versuchsreihe, eine befriedigende Übereinstimmung. Theoretisch müßte auch hier die der Lösung entzogene K-Menge etwas geringer sein als die K-Menge in der Pflanzensubstanz, da das junge Pflänzchen schon beim Ansetzen etwas K enthielt. Wenn man jedoch berücksichtigt, daß die Pflänzchen zu Beginn des Versuches höchstens 2 g wogen, bei der Ernte die Frischgewichte einer Pflanze aber ca. 200 g betrugen, so ist der Anteil des bereits vorher in der Pflanze vorhandenen K selbst bei hohem K-Gehalt vergleichsweise gering.

In den Reihen mit Blattdüngung wurden nur ca. $\frac{3}{4}$ des gesamten in der Pflanze enthaltenen K von der Wurzel aufgenommen, der Rest entstammt der extraradikalen K-Gabe. Die Möglichkeit, daß von den Blättern darüberhinaus noch mehr K sorbiert, dann aber weiter über die Wurzeln bis in die Nährlösung transportiert wurde, ist nicht ausgeschlossen. Es fällt auf, daß in den Reihen K_BMg_2 weniger K aus der Nährlösung aufgenommen wurde als in den Reihen K_BMg_1. Man kann vermuten, daß dieser Unterschied durch den höheren Mg-Gehalt der Nährlösung und der Pflanze bewirkt wurde, der sowohl auf die radikale Sorption als auch auf den K-Transport stärker konkurrierend gewirkt hat und damit eine vergleichsweise geringere K-Aufnahme über die Wurzel hervorrief.

f) *Der Einfluß der höheren Mg-Düngung (Mg_2) auf den Gehalt an Ca, K und Na*

In Figur 4 sind die Ca-, K- und Na-Gehalte der höheren Mg-Düngung (Mg_2) mit den entsprechenden Gehalten bei der Düngung Mg_1 verglichen. Hierbei wurden die Werte der Reihen $Mg_1 = 100$ gesetzt. Es ist ersichtlich, daß die Gehalte der Reihen Mg_2 um die „Linie 100" schwanken. Man kann also weder bei den Wurzeln noch bei den Stengeln oder Blättern einen gesicherten Einfluß der Mg-Düngung auf die Gehalte der anderen Kationen feststellen. Betrachtet man jede einzelne Pflanze für sich, so sieht man, daß zwar in den meisten Fällen die Mg-Düngung zumindestens in einem Pflanzenorgan (Blatt, Stengel, Wurzel) den Gehalt der übrigen 3 Kationen negativ beeinflußt hat, jedoch sind die Unterschiede nicht sehr überzeugend. Hiermit sei nicht gesagt, daß das Mg-Ion keinen konkurrierenden Einfluß auf andere Kationen haben könnte. Die Differenz zwischen der Düngergabe Mg_1 und Mg_2 be-

trägt ca. 4 mmol, die zwischen K_1 und K_2 ist dagegen etwa 10 mal so groß. Da aber die Stärke von Ionenkonkurrenzen wesentlich von der Ionenkonzentration abhängt, wird verständlich, daß die konkurrierende Wirkung des Mg-Ions infolge seiner niedrigen Konzentration im vorliegenden Fall nicht deutlich wird.

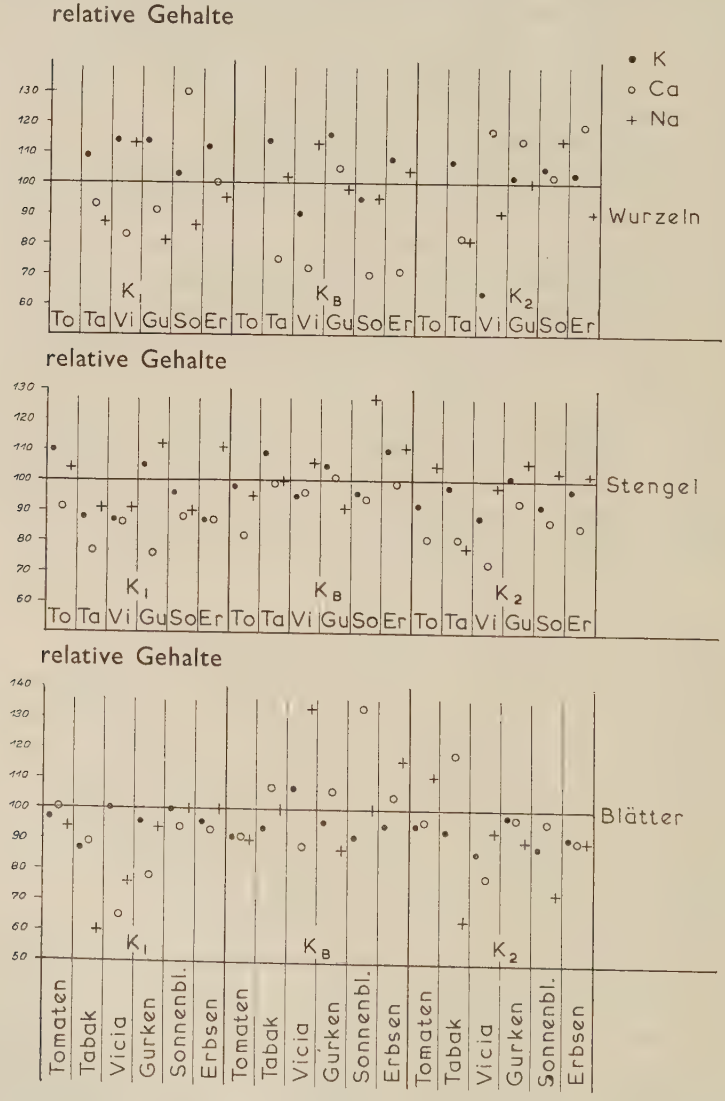

Fig. 4. Der Einfluss einer höheren Mg-Gabe (Mg_2) auf den Gehalt an K, Ca, und Na ($Mg_1 = 100$).

4. BESPRECHUNG DER ERGEBNISSE

Die gegenseitige Beeinflussung der Kationen bei ihrer Aufnahme und Verteilung physiologisch zu deuten, ist schwierig, da die Pflanze und auch ein Pflanzenorgan kein einheitliches chemisch-physikalisches System darstellt, und da in einer Analyse nur die Ionenverhältnisse des betreffenden Erntetages, nicht aber die gesamte Dynamik der Kationenaufnahme im Verlauf der Vegetation zum Ausdruck kommen.

Es darf als sicher angenommen werden, daß die ältere Anschauung über den Einfluß der Ionen auf die Permeabilität lebender Membranen (Quellung, Entquellung) [2 18] nicht ausreicht, um die gegenseitige Beeinflussung der Ionen bei ihrer Aufnahme und Verteilung zu erklären [1]. Die mit den älteren Theorien verbundenen Bezeichnungen „Antagonismus" und „Synergismus" können deshalb verwirrend wirken, zumal sie in der Literatur auch unterschiedlich definiert werden [14 17 22].

Es ist somit zweckmäßiger, von einer konkurrierenden Wirkung der Ionen zu sprechen. Die Tatsache, daß bei verstärktem Angebot einer Kationenart andere Kationen in geringerem Maße aufgenommen und in der Pflanze transportiert werden, kann man damit erklären, daß die Kationen untereinander um organische negative Valenzen – wahrscheinlich in erster Linie um die indiffusiblen Anionen des Plasmas – konkurrieren [8]. Die Ionenkonkurrenz wird also dadurch charakterisiert, daß das in höherer Konzentration vorliegende Kation andere Kationen von ihren sorptiven Bindungsstellen verdrängt, bzw. negative Valenzen absättigt, die dann anderen Kationen nicht mehr zugänglich sind. Epstein *et al.* [10 11] sowie Fried und Noggle [12] und Legett und Epstein [16] haben derartige Ionenkonkurrenzen an abgeschnittenen Gerstenwurzeln für die verschiedensten Ionen nachweisen können. Bei diesen Untersuchungen handelt es sich um eine Konkurrenz um die negativen Valenzstellen der Trägersysteme der Wurzel, woraus hervorgeht, daß nicht nur die Sorption, sondern auch der Transport mit der konkurrierenden Wirkung der Ionen im Zusammenhang steht.

Man darf annehmen, daß die vier zur Diskussion stehenden Kationen mindestens in drei verschiedenen Formen in pflanzlichen Geweben vorkommen können: a) Als freie Ionen z.B. in der Vakuole, im Xylemsaft oder auch im Zytoplasma. b) Als adsorptiv gebundene

Ionen, z.B. an Valenzen des "free space" [3 13], an Eiweißstrukturen innerhalb des Zytoplasmas [19] oder auch an spezifische Träger [9]. c) Als feste Bausteine einer organischen oder anorganischen Verbindung, z.B. Mg im Chlorophyll oder Ca in Ca-Oxalatkristallen.

Dieser unterschiedliche Bindungszustand weist daraufhin, wie problematisch es ist, aus dem Gesamtgehalt an einzelnen Kationen auf die Intensität von Ionenkonkurrenzen schließen zu wollen. Gewebe, die hohe Mengen verschiedener Kationen als feste, nicht adsorptiv gebundene Bausteine inkorporiert haben, sind deshalb für das Studium von Ionenkonkurrenzen ungeeignet, es sei denn, man trennt die adsorptiv gebundenen Ionen vor ihrer eigentlichen Analyse ab. Gewebearten, die dagegen hohe Konzentrationen indiffusibler Ionen (z.B. plasmareiche Gewebe) neben geringen Mengen anderweitig fest inkorporierter Kationen und darüber hinaus auch ein geringes Volumen an freier Lösung aufweisen, werden die in vivo vorliegende konkurrierende Wirkung der Ionen am besten zeigen. Diese Überlegung erklärt, weshalb gerade die Kationengehalte der holzigen Stengel von Tabak und von Vicia keine Ionenkonkurrenz erkennen lassen. Offenbar war hier der Anteil fest eingebauter Ionen und besonders das Volumen an freier Lösung (Xylemsaft und Phloemsaft) so groß, daß die Ionenverhältnisse der relativ wenigen adsorbierten Ionen in der Analyse nicht mehr erkenntlich sind.

Bei der vorliegenden Untersuchung wurde absichtlich mit mehreren Pflanzen gearbeitet, um Zufälligkeiten, die eine Ionenkonkurrenz vortäuschen können, nach Möglichkeit zu vermeiden. Wenn darüber hinaus noch zwei verschiedene Nährlösungen verwendet wurden und der Wechsel der Nährlösung während der Vegetation für die einzelnen Pflanzenarten ebenfalls unterschiedlich gehandhabt wurde, so kann man der bei unterschiedlichen Bedingungen resultierenden Reaktion der einzelnen Pflanzenarten auf eine Düngungsmaßnahme eine gewisse allgemeine Gültigkeit zusprechen, falls die Versuchserbegnisse für alle Pflanzen die gleiche Tendenz aufweisen. Auf die Frage, in welchem Pflanzenorgan die Ionenkonkurrenz am stärksten ist, darf deshalb geantwortet werden:

Die Ionenkonkurrenz zeigt sich am stärksten im Blatt. Auch in Stengel und Wurzel spielen sich entsprechend der oben dargestellten Anschauung Ionenkonkurrenzen ab, die Kationenverhältnisse können hier jedoch noch von anderen Faktoren nachhaltig be-

einflußt werden, so daß auch bei höherer K-Düngung die Gehalte der übrigen Kationen in Wurzel und Stengel ansteigen können (siehe Figur 2).

So wird die augenblickliche Konzentration an Kationen in der Nährlösung, die sich durch unterschiedlichen Entzug an verschiedenen Kationen im Laufe der Vegetation wesentlich ändern kann, für die im Augenblick vorliegenden Kationengehalte der Wurzel von Bedeutung sein.

Für die Kationenverhältnisse im Stengel ist zu berücksichtigen, ob im gegebenen Moment die Ionenkonkurrenz im Blatt oder in der Wurzel dominierend ist. Ist z.B. schon eine starke Konkurrenz um Trägervalenzen in der Wurzel zwischen zwei Kationen gegeben, so wird der Xylemsaft und damit die Analyse des Stengels auch diese Konkurrenz zeigen, falls der Transport aus dem Xylemsaft in anderes Gewebe nicht allzu wesentlich durch konkurrierende Wirkungen beeinflußt wird. Unsere frühere Feststellung [26], daß die höhere K-Konzentration den Ca- und Mg-Gehalt der Blätter erniedrigt, den der Stengel aber erhöht hat, dürfte somit ein Einzelfall sein, bei dem die Ionenkonzentration im Blatt dominierend war.

Die Depression der Ca-, Mg- und Na-Gehalte des Blattes bei extraradikaler K-Gabe ist sicherlich nicht durch eine verminderte Transpiration in den besprühten Blättern hervorgerufen worden, da man sonst auch im Stengel eine ähnliche Tendenz hätte feststellen müssen. Darüber hinaus hat nach neueren Anschauungen die Transpiration nur einen unwesentlichen Einfluß auf den Ionentransport [5 6]. Mit markierten Lösungen konnten wir ebenfalls in kurzfristigen Versuchen, über die an anderer Stelle noch berichtet wird, feststellen, daß eine K-Blattdüngung den Eintritt von Ca^{45} in das Blatt behindert. Die Vergleichsreihe wurde in diesem Fall mit H_2O besprüht, um die Wirkung der Transpiration zu eliminieren.

Wir dürfen also annehmen, daß die vergleichsweise niedrigeren Gehalte an Mg, Ca und Na der Blätter auf die konkurrierende Wirkung des extraradikalen K zurückzuführen sind. Hierbei bleibt die Möglichkeit offen, daß zwischen Xylemsaft und Blattgewebe Trägersysteme existieren, um die die einzelnen Ionen konkurrieren können.

Brouwer [4] verweist ebenfalls darauf, daß die Aufnahme von Ionen von dem Salzzustand des betreffenden Pflanzenmaterials abhängig ist; Scott Russel u. Ayland [23] stellten fest, daß der K-

Gehalt verschiedener Gewebe einen merklichen Einfluß auf die Rb-Aufnahme hat.

Das Zytoplasma, wie auch alle übrigen Zellbestandteile, die negative Valenzen tragen, kann man mit Metzner [19] als einen Anionenaustauscher auffassen. Man muß jedoch hierbei im Auge behalten, daß auf Grund unterschiedlicher plasmatischer Strukturen die Valenzen untereinander nicht gleichwertig sind [20]. Es muß also angenommen werden, das es Valenzen gibt, die eine bestimmte Art von Kationen bevorzugen, wobei es wahrscheinlich ist, daß neben ionogenen Kräften auch chelatartige Bindungskräfte mitwirken.

Aus Tabelle 3 geht hervor, daß die Konzentration des Na meistens in den Wurzeln am höchsten ist. Es darf deshalb angenommen werden, da ein niedriger Na-Gehalt in den oberirdischen Organen auf ein beschränktes Na-Trägersystem schließen läßt, daß das Na in der Wurzel hauptsächlich im "free space" in adsorptiv gebundener Form vorliegt. Die Ionenkonkurrenz des Na gegenüber K in der Wurzel (Figur 2) dürfte also hauptsächlich im "free space" lokalisiert sein. Dagegen liegt gerade in den Pflanzen, die einen niedrigen Na-Gehalt aufweisen (Erbsen und Sonnenblumen) in den Blättern keine Ionenkonkurrenz vor. Offenbar werden hier die geringen Na-Mengen von spezifischen Na-Bindungsstellen sorbiert, oder aber das Na liegt praktisch nur in freier Ionenform vor. Vicia, Tabak, Gurken und Tomaten haben wesentlich höhere Na-Gehalte, und hier ist auch im Blatt eine Ionenkonkurrenz zwischen Na und K ersichtlich. Die Beobachtung, daß die konkurrierende Wirkung des Na nur bei Pflanzen mit höherem Na-Bedarf vorliegt, deckt sich mit den Ergebnissen anderer Autoren [15].

ZUSAMMENFASSUNG

1. An sechs verschiedenen zweikeimblättrigen Pflanzen wurde in Wasserkulturversuchen untersucht, wie eine gesteigerte radikale und eine gesteigerte extraradikale K-Düngung sowie eine erhöhte radikale Mg-Düngung den Gehalt der Wurzeln, Stengel und Blätter an Ca, Mg, K und Na beeinflußt.

2. Die Ionenkonkurrenz des K gegenüber Mg und Ca zeigte sich bei der höheren radikalen K-Düngung am besten in den Blättern. Auch in den Stengeln und Wurzeln bewirkte sie in den meisten Fällen einen geringeren Ca-, Mg- und Na-Gehalt.

3. Die Ionenkonkurrenz zwischen K und Na war am deutlichsten in den Wurzeln ausgeprägt.

4. Die zusätzliche extraradikale K-Gabe hatte lediglich einen negativen Einfluß auf die Ca-, Mg- und Na-Gehalte der Blätter. Stengel und Wurzel wurden dagegen in ihrem Kationengehalt durch sie nicht beeinflußt.

5. Die Wirkung der erhöhten radikalen Mg-Düngung auf den Gehalt an Ca, K und Na war nicht eindeutig.

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